Assembly rules in grassland plant communities

DISSERTATION ZUR ERLANGUNG DES DOKTORGRADES DER
NATURWISSENSCHAFTEN (DR. RER. NAT.)
DER FAKULTÄT FÜR
BIOLOGIE UND VORKLINISCHE MEDIZIN DER UNIVERSITÄT REGENSBURG

VORGELEGT VON

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im Jahr 2011

Promotionsgesuch eingereicht am: 13.7.2011

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Chapter 1

General introduction

Why does a plant grow where it grows? Why do plant community assemblies follow one path or another in a given environment? These questions were raised by the first ecologists and still challenge plant ecological research today. Facing problems to maintain and restore valuable plant communities, an understanding of the mechanisms and rules driving species assembly has become even more urgently needed (Temperton *et al.* 2004).

Assembly rules

The observation that local plant communities are composed by subsets of species available in the regional species pools raised the question if this subset may be predictable given the species of the regional pool and the local environmental conditions. The term “assembly rule” for this kind of predictions was first coined by Diamond (1975). He stated that bird communities on islands should contain fewer species combinations than expected by chance and that it was predictable which species sets were able to coexist (“allowed combinations”) and which were not (“forbidden combinations”).

Working out “assembly rules” it is necessary to be aware of the filters which act on the single species and which decide over species access to the given species pool.

An illustrative model depicting the single filters which sort the species that could enter to a local species pool was set up by Fattorini and Halle (2004) (figure 1). According to their dynamic environmental filter model the number and identity of species “waiting at the entrance” of a particular community is determined by large scale processes like speciation, migration and dispersal ("species pool concept", Zobel 1992; Zobel 1997). The pool of established species consists of species of the external species pool, i.e. species that may invade by dispersal from the surroundings, and of species counting to the internal species pool, i.e. in the case of plant communities, species from the seed banks. Established species first had to pass an abiotic filter (chemical and physical environmental conditions) which defines the fundamental niche of a plant species. Only if a species passed this filter, it can enter the struggle for life with the resident species (biotic filter).

Furthermore, internal feedback loops exist such that the established species shape the abiotic conditions at a site, e.g. by litter production, or such that disturbances change the strength of the biotic filter, e.g. by weakening strong competitors.
Whether a plant species succeeds to pass the abiotic and the biotic filter of a site is largely confined by the traits of the plant.

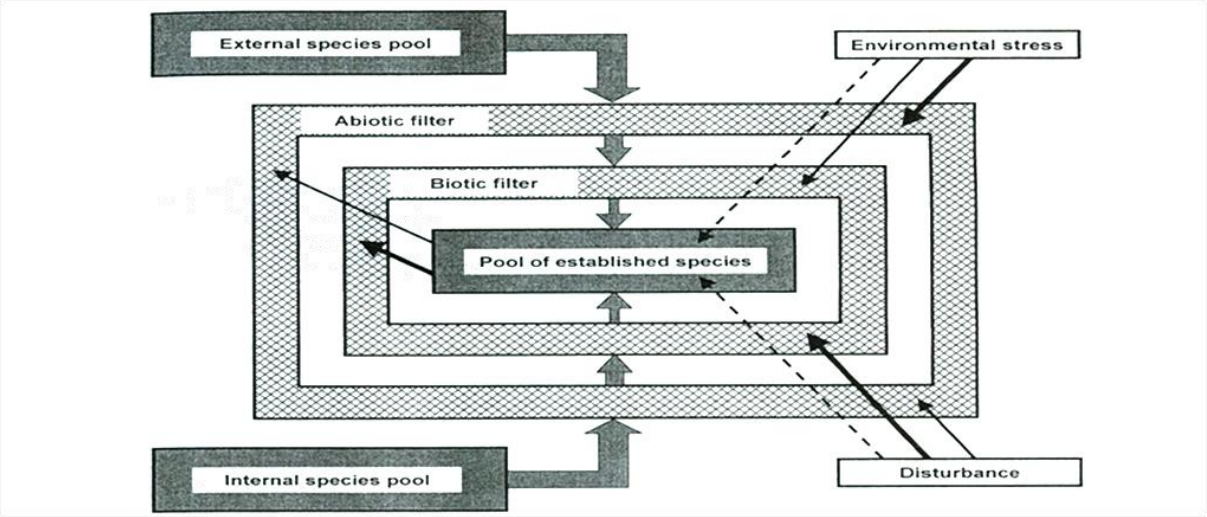

Figure 1: The dynamic environmental filter model. New species can invade by dispersal from the surroundings (external species pool) or from the seed bank (internal species pool). For successful invasion species have to pass the abiotic filter and the biotic filter. Internal feedback loops and external cues (environmental stress and disturbance) constantly readjust the filter mesh sizes. Thickness of the arrow lines indicates the strength of the effect (Fattorini & Halle 2004).

Plant functional traits

Plant traits are biological characteristics of plant species like morphological or regenerative features (Weiher *et al.* 1999; Violle *et al.* 2007). It is a consequence of natural selection that plant species are adapted to their natural habitats based on their traits. Different environments demand different adaptations and select different traits. Plant traits determine if a plant can germinate, establish and increase in abundance under specific environmental conditions or processes like disturbance, land-use, climate change etc.. A plant trait that is filtered out by the given environment is defined as functional. It is a logical consequence to search for assembly rules by using plant traits as link between environmental conditions and species occurrences. With plant traits as filtering units of the filters implied in the previous filter model, it is possible to establish trait based rules of community assembly. Trait based rules in turn provide not only insight into filtering mechanisms, but also may be applied over a broad range of environments.

Former approaches of this kind were the explanation of plant distributions applying the life forms of, for example, von Humboldt (von Humboldt 1805; in Clements 1928), Warming (Warming 1909; in Clements 1928) Raunkiaer (Raunkiaer 1905; in Clements 1928) or Grimes CSR strategy types (Grime 1979).

Today, more comprehensive information on plant traits is available in plant trait databases like LEDA (Kleyer *et al.* 2008), BIOPOP (Poschlod *et al.* 2003; Jackel *et al.* 2006), CloPla3 (Klimešová & de Bello 2009) or the Electronic Comparative Plant Ecology (Grime *et al.* 1988; Hodgson *et al.* 1995) offering new prospects for the field of assembly rules research.

Opportunities and limitations of the trait based approach

Opportunities

The trait based approach for explaining species responses to different processes or species occurrences or abundances in different environments can be applied to all kinds of organisms. Several studies applied a multitude of approaches and analysis methods to search for assembly rules in the plant kingdom – looking for guild proportionality (e.g. Silvertown 1980a; Wilson 1989; Wilson & Watkins 1994; de Kroon & Olff 1995; Wilson & Gitay 1995a; Wilson *et al.* 1996; Silvertown *et al.* 2006), selection for trait convergence or divergence (e.g. Watkins & Wilson 2003; Cowling *et al.* 2005; Fukami *et al.* 2005; Grime 2006), selection for single functional traits (e.g. Bullock *et al.* 2001; Díaz & Cabido 2001; Kahmen & Poschlod 2004; Vesk *et al.* 2004a; Díaz *et al.* 2007; Garnier *et al.* 2007; Kahmen & Poschlod 2008b) or for functional groups (e.g. Grime 1974; Kleyer 1999; Pillar 1999; Kleyer 2002; Keith *et al.* 2007; Römermann *et al.* 2009). Altogether, these studies demonstrated the broad range of opportunities that trait based approaches provide to shed lights upon the mechanisms of community assembly and to reveal general trends of trait based species selection for various kinds of processes and habitats.

Concerning the processes that were analysed in the different studies, results are available on trait based species selection due to climate change (Skarpe 1996; Díaz & Cabido 1997; Arft *et al.* 1999), due to disturbance (McIntyre *et al.* 1995; Lavorel *et al.* 1998), due to land-use (e.g. Landsberg *et al.* 1999; Díaz *et al.* 2001; Dupré & Diekmann 2001; Moog *et al.* 2005; Díaz *et al.* 2007; Gross *et al.* 2007; Pakeman *et al.* 2008; Römermann *et al.* 2009; Pakeman & Marriott 2010), in ecological restoration (Pywell *et al.* 2003; Fagan *et al.* 2008) or in invasion biology (e.g. Rejmanek & Richardson 1996; Winter *et al.* 2008; Roscher *et al.* 2009b).

Limitations

While the trait based approach offers ample new insights into plant community assembly, the predictability of plant species response and community composition based on "assembly rules" and a given species pool remains a critical issue. The complexity of interactions between plants and their biotic and abiotic environment are the major constraints in predicting vegetation responses to processes like climate change or disturbance (Körner 1993). Accordingly, the prediction of extinction risk (Freville *et al.* 2007) or plant response to management (Vesk & Westoby 2001) based on plant traits proved to be hindered by the multitude of site specific extrinsic factors and many studies confirmed the stochastic models of community assembly (Harper 1977; Zobel 1992; Hubbell 2001), which imply Gleasons´s (1926) individualistic model. Those non-deterministic models predict non-repeatable vegetation development driven by dispersal limitation, order of establishment or abundance feedbacks, with outcomes often determined by which species arrived first and in which abundance.

Limited reliability of trait based predictions has been explained by Baker (Baker 1965; in Noble 1989) on the example of plant species´ invasion potential: "…an ideal weed is a plastic perennial which will germinate in a wide range of physical conditions, grow quickly, flower early, is self-compatible, produces many seeds which disperse widely, reproduces vegetatively and is a good competitor." However, as Baker pointed out, no one species needs all these features to be a successful invader. Conversely, the possession of a single, or indeed several, characters from the list does not mean the species will be a successful invader (Noble 1989).

Maybe the limitations of assembly rules research are best relativized by scaling down the expectations on those rules. It would be unwise to claim the rules to be more than general trends, like it is true for other ecological rules (Allen´s rule, Bergmann´s rule etc.) (Booth & Larson 1999). A nice analogy brought up by Shipley (2010) is to look at the process of community assembly as nature-as-a-biased-die with a resulting model of community assembly through chance constrained by natural selection. Therewith, we should not expect those rules to formulate more than trait based probabilities of species success or failure in a given environment.

Thesis outline

This thesis is part of the collaborative project ASSEMBLE within the ESF-Eurodiversity Programme (05_EDIV_FP040-ASSEMBLE) and was financially supported by the German Science Foundation (PO 491/5-1), the European Science Foundation and by the Agency for the development of agricultural landscapes (LEL) in Baden-Württemberg.

The objective of the ASSEMBLE-project was to "understand the rules that govern the assembly of local plant communities from the species available in fragmented landscapes, based on functional traits, with a focus on generalizations across particular systems."

There are different perceptions of what an "assembly rule" should look like. While one group of today´s ecologists explicitly defined an assembly rule as "a restriction on species presence or abundance that is based on the presence or abundance of one or several other species, or types of species (not simply the response of individual species to the environment)." (Diamond 1975; Wilson & Watkins 1994; Wilson & Gitay 1995b; Wilson & Whittaker 1995), others, like Keddy (1992) or Drake (1990; 1993), include mechanisms on species sorting based on climatic conditions, disturbance regime and biotic interactions. Booth and Larson (1999) noted on this topic that the current language on the "assembly rule" framework has become unnecessarily complex and that the fixation on Diamond´s term "assembly rules" may further run the risk of reinventing well established ideas, as already Clements (1928) and Gleason (1926) worked on plant community assembly - unless they called those rules developmental constraints.

In this thesis I took "assembly rules" as any developmental constraint on the plant community structure including abiotic as well as biotic constraints. Therefore, this study deals with the same questions that have been asked consistently since the 19th century. The new perspective on these questions is the way we can approach them today. Taking advantage of trait databases, which comprise traits related to all aspects of plant life of the vast majority of northwestern European plants, we can now go to explain "plant behaviour" and community assembly by a great variety of traits and determine which single trait or set of traits may be important for the establishment and success in a certain environment.

The ecosystem I put into focus to work out "assembly rules" were grasslands in southwest Germany (Baden-Württemberg). The studied grasslands constitute remnants of a formerly connected open farming landscape. They were created by human activities - deforestration followed by livestock grazing or mowing - since the Iron Age and first expanded during Roman times (Poschlod & WallisDeVries 2002). In the course of their formation semi-natural

grasslands offered new habitats for numerous species which were formerly restricted to marginal habitats, like rocky outcrops, open woods, river banks etc. (Zoller 1954; in Wilmanns 1998). Especially calcareous grasslands rank as one of the most species rich communities at a small scale (WallisDeVries *et al.* 2002 and citations therein). Nevertheless, not only calcareous grasslands but all kinds of extensively used grasslands are threatened and of high conservation value today. Industrialization of agriculture during the 20th century led to losses of traditionally used grasslands due to intensified use including fertilization, drainages, liming but also abandonment of less profitable sites (Poschlod & Schumacher 1998; Poschlod *et al.* 2009a). All remnant semi-natural grasslands are fragile habitats as their continued persistence depends on some form of management. It is up to discussion what the best management regime for particular species or groups of species is. Furthermore, fragmentation poses threats of extinction and inbreeding effects for remaining populations (Fischer & Matthies 1997; Fischer & Stöcklin 1997).

The current thesis deals with assembly processes of grassland plant communities dependent on management treatment (chapters 2, 3, 4) and site history (chapter 6), while chapter 5 puts the focus on mechanisms of small scale assembly processes.
Therewith, the thesis was predestined to link basic assembly rules research with questions concerning grassland conservation and restoration. Chapter 7 serves this purpose giving conclusions and perspectives for conservation and restoration practice based on the results of the previous chapters.

In chapter 2 (**Adaptation of plant functional group composition to management changes in calcareous grassland**) long-term vegetation data of a formerly homogeneously grazed grassland, on which different management treatments were installed about 30 years ago, were analysed. I aimed to understand changes in plant species composition after management change (1) by finding functional groups that react, i.e. are functional, with regard to the analysed disturbance gradient and (2) by following the functional group composition over time as adaptation to the changed disturbance regime. Therewith, mechanisms behind changes in plant species occurrence and abundance should be revealed.

Chapter 3 (**Winner and loser plants in differently managed grasslands: a trait-based approach**) was explicitly designed to filter out management specific trait selection mechanisms over different grassland types. Therefore, longterm-vegetation data of grasslands belonging to different associations and subjected to different management treatments for ca.

30 years were analysed. By contrasting species that went extinct over the time with invaded species for different management treatments, management specific trait selection patterns could be studied.

Management dependent trait selection should be put to test by a sowing experiment (chapter 4: **Limitations to plant establishment in differently managed calcareous grassland**). Low establishment success complicated proper conclusions on trait based species success or failure at different management treatments and moreover illustrated the constraints of the trait based approach to predict single species success by knowing the selection mechanisms acting at the different management treatments. Therefore, we changed the direction of the analysis of this experiment and elucidated the roles of the management specific filter mechanisms to cause germination niche limitation or to influence seedling survival.

Despite the low establishment success in the sowing experiment, some patterns regarding the importance of the invaders´ neighbourhood on establishment success could be revealed (chapter 5: **Neighbourhood impact on plant invasion success in a calcareous pasture**). Therefore, we analysed vegetation and a multitude of factors on a small scale around the sown subplots to find hints for neighbourhood indcuced establishment patterns.

Another field addressed in chapter 6 **(Land use history, functional traits and biotic filter – which factors cause indicator species status in ancient and recent calcareous grasslands?**) is the restoration of grasslands on ex-arable fields. Agricultural intensification not only led to destruction of extensively used grasslands but also to abandonment of arable fields at less favorable sites. It is of most concern within the field of restoration ecology to restore valuable grasslands at those sites. Nevertheless, restoration to a state that resembles ancient grasslands turned out to be complicated. By comparing nearby ancient grasslands and grasslands on ex-arable fields with a trait-based approach, reasons for restricted occurrences of indicator species of ancient and recent grasslands should be worked out.

Finally, the results of the previous chapters were reviewed with regard to their implications for conservation and restoration practice (chapter 7: **Linking assembly rules with nature conservation and restoration practice**).

Chapter 2

Adaptation of plant functional group composition to management changes in calcareous grassland

Abstract

It is the aim of plant functional research to generate general rules of species assembly and species reactions based on plant functional traits. Here we determined plant functional groups that are important with regard to land use types (grazing, mowing, mulching, burning, abandonment) and looked for mechanisms leading to changes in species composition after management changes in calcareous grasslands.

To filter out the set of traits which best described the variation in plant composition along the studied land use gradient and to identify functional groups we chose an iterative three-table ordination method. We included traits related to persistence as well as traits describing the germination niche of a plant. To gain insight into underlying mechanisms which led to differing importance of these plant functional groups at different management regimes we investigated shifts in dominance of the identified functional groups at eight management regimes using long-term vegetation data of a site which was grazed before the onset of different management regimes in 1974. Ongoing unidirectional changes in cover of the four determined functional groups at most of the treatments indicated that even after almost 30 years new equilibria of functional group composition were still not reached.

The study showed that other management treatments but grazing and mowing led to changes in functional group composition, which were mainly driven by increasing dominance of a highly competitive species group.

Introduction

Semi-natural grasslands in Northwestern Europe evolved mainly under grazing management. Their high diversity in flora and fauna makes them extremely valuable for nature conservation (Willems 1983; WallisDeVries *et al.* 2002). Due to loss of agricultural usefulness calcareous grasslands suffered strong decreases during the 20th century and were put in the focus of conservation efforts (Poschlod & WallisDeVries 2002; Poschlod *et al.* 2005a). In the course

of this development the fallow experiments Baden-Württemberg were initiated in 1974 to test the capability of cost-effective management treatments like mulching and burning regimes to maintain this vegetation which also includes a great number of rare and endangered species. This project encouraged a range of studies on management induced vegetation changes analysing species reactions based on their phytosociological affiliation as well as studies focusing on plant functional traits (Schiefer 1981, 1983; Kahmen *et al.* 2002; Moog *et al.* 2002; Kahmen & Poschlod 2004; Moog *et al.* 2005; Schreiber 2005, 2006; Kahmen & Poschlod 2008b; Römermann *et al.* 2009). Those functional approaches help to reveal underlying mechanisms leading to changes in plant species composition that could hardly be detected by taxonomic approaches. In case of the fallow experiments clear results were found for the functional trait development under succession. Over all 14 study sites included in the fallow-experiments tall species were promoted, as well as species with regular leaf-distribution, high vegetative lateral spread, late flowering and high seed mass (Kahmen & Poschlod 2004). Abandonment and burning treatments favoured spring germination (Kahmen *et al.* 2002). Enhancement of certain germination strategies after management change was also found for other study sites (Olff *et al.* 1994). Poschlod et al. (1998) pointed out that dispersal and seedbank features are also crucial for maintenance and re-establishment of calcareous grasslands.

Predicting vegetation development to a changing environment based on plant traits is a helpful tool in nature conservation practice. It provides the opportunity to adjust management treatment to enhance target species with certain traits or functional group affiliation (Jackel *et al.* 2006). Plant functional groups are groups of species that share functional trait attributes and due to those respond to environmental gradients in similar way (Lavorel *et al.* 1997; Semenova & van der Maarel 2000).

Nevertheless, the difficulty to predict species response at a given environment becomes apparent, when the response of single species to one disturbance regime differs between different sites: Vesk and Westoby´s metaanalysis of plant species response to grazing (Vesk & Westoby 2001) showed, that 41 % of the tested species responded inconsistently.

We used a comprehensive vegetation dataset of the year 2000 to identify plant functional groups that co-occur in differently managed plots in dry grasslands. We used the RLQ-analysis, a three table ordination method, linking vegetation relevés, species traits and environmental information (Dolédec *et al.* 1996) to identify these plant functional groups. The

best set of traits was determined using iterative RLQ as proposed by Bernhardt-Römermann *et al.* (2008).

With these functional groups we aimed to gain better insights into underlying mechanisms leading to changes in species composition by viewing the development of the determined plant functional groups over time after management change using a set of long-term vegetation data. Unidirectional trends in plant functional group cover development over time should also verify the importance of the obtained functional groups for changes in plant species composition.

We aim to unravel the mechanisms that led to changes in plant functional group composition of different management regimes by addressing following questions:

Which functional groups can be identified with regard to different grassland management treatments?

How did these plant functional groups change in relative importance at different management treatments over time?

Materials and methods

Study site

The study site, a species-rich calcareous grassland, is located in Southwest Germany and part of the fallow experiments Baden-Württemberg, which were initiated by Prof. Karl-Friedrich Schreiber in 1974. On the study site the practicability of alternative management regimes to the traditional grazing or mowing regimes has been tested, with focus on their capability to maintain the high species richness and typical plant species composition.

The study site has a long sheep-grazing history and thus featured homogeneous, species-rich vegetation at the beginning of the experiment. The site is located on the Swabian Alb (760 m NN, annual precipitation 1000 mm, mean temperature 7.6 °C, exposition WSW, inclination 5-15 %). At the beginning of the experiment in 1975 the site was split in several fields lying next to each other with a small gap in between (field sizes range from approx. 630 m² to 2400 m²). On each of these different management treatments were continuously applied. As control the historical land-use was continued on one field by extensive sheep grazing for 1-2 weeks twice per year (150-200 sheep/ha). On further sections the following treatments were started in 1975: mulching twice per year (early and late summer), mulching once per year (late summer), mulching every second year (late summer), burning once per year (in winter) and abandonment. Mulching resembles mowing but the phytomass is chopped and left on the site.

Burning every second year (in winter) was additionally started in 1978 after dividing the once per year burnt field into the two burning treatments (burning once per year and every second year). Mowing once per year was only installed in 1981, following some years of succession, as it was not included in the originally planned set of treatments, which aimed to substitute the traditional but costly management regimes grazing and mowing.

Data

Vegetation data

Two sets of vegetation data were used for our analysis. The first data-set was used to detect which traits are most useful to describe differences between management treatments, while the second was used to describe the functional development of each treatment over time. This separation was needed because per vegetation treatment only one permanent plot exists which is too less for a proper detection of the most important traits. Thus, we used a data-set from 2000, which contains 8 plots per treatment.

(1) Per treatment eight relevés of 2m x 2m plots were taken for the plant functional group extraction using RLQ-analyses. Vegetation was sampled in the year 2000 on eight plots per treatment that were evenly distributed over each management field.

(2) To unveil the functional mechanisms behind changes in plant composition a second dataset consisting of long-term vegetation data was used. This dataset comprises vegetation relevés of one permanent plot of 5m x 5m per management treatment, which was installed at the beginning of the experiment. Vegetation relevés of these permanent plots were carried out regularly with a maximum gap of five years in between (covered time span: 1975 – 2004).

All vegetation relevés were recorded using the Schmidt scale (Schmidt *et al.* 1974) with an additional category of 0.1 % cover (table 1). For all our analyses we focused on the herb layer without shrub and tree regeneration. Shrubs and trees only reached adult stages at the abandoned field, while records at all treated fields referred to seedling stages of shrubs and trees. Hence, including traits of the adult stages in our analyses would have complicated to find meaningful functional groups.

Environmental data

The management gradient was described by several environmental factors. Available information on environmental data included percentage cover and height of moss and litter layer. Additionally, we calculated mean weighted Ellenberg indicator values per vegetation relevé for nutrients (N), light (L), moisture (F) and reaction (R) (Ellenberg *et al.* 2001) as

substitutes for missing direct measurements of these factors. The Ellenberg indicator values are species-specific scores ranging from 1-9 (or 1-12 for moisture) and estimate the optimum ecological occurrence of species along environmental gradients (Ellenberg *et al.* 2001). Evidence for the accuracy of these indicator values was provided by several studies reporting a close correlation between the indicator values and corresponding measurements of environmental variables on large gradients (Schaffers & Sýkora 2000; Diekmann 2003). As suggested by Wamelink et al. (2002), we used Ellenberg indicator values for comparisons within the same vegetation type.

Trait data

Data on plant traits were extracted from the databases LEDA (Knevel *et al.* 2003, www.leda-traitbase.org; Kleyer *et al.* 2008), BIOPOP (Jackel *et al.* 2006, www.floraweb.de/proxy/biopop/de/index.php) and CloPla3 (Klimešová & de Bello 2009, http://clopla.butbn.cas.cz) (table 1).

If more than one data entry for one species was available for one trait, we took the mean out of these values for metric traits. Categorical traits were ranked according to appropriate rules (e.g. when several entries on seed shedding times were available, we took the earliest mentioned month as month of seed shedding start and the latest mentioned month as month of seed shedding end).

Data analyses

Extraction of plant functional groups

To identify functional groups with different importance at different management regimes and accompanied environmental conditions, we chose the RLQ-analysis, a three table ordination method, linking vegetation relevés, species traits and environmental information (Dolédec *et al.* 1996). In RLQ information on environmental conditions (R-table: sites x environment) is linked to plant trait-data (Q-table: species x traits) by the vegetation relevés (L-Table: species x sites). In preparation for the RLQ, the first step is a correspondence analysis (CA) performed on the L-table after arcsine-square root transformation of the percentage cover values. Next, mixed ordinations (Hill Smith ordinations, Hill & Smith 1976) are carried out on the R-table using the row scores of the CA on L-table as canonical factor and on the Q-table using the column scores of the CA on the L-table as canonical factor. The RLQ calculates two separate co-inertia analyses, one between the constrained ordination on the Q-table and the CA on L and the second between the constrained ordination on the R-table and

the CA on L. In an iterative process RLQ-axes are determined, which display maximum covariance between the Q- and the R-axes.

In the R table we included the management treatment as a nominal variable reflecting the whole sum of management induced environmental differences. In a second step we determined the most meaningful set of numerical environmental variables out of the available parameters by calculating maximum rank correlation between the L-table and all possible sets of environmental variables. This method is explained in Clarke & Ainsworth (1993). The best subset of environmental parameters included Ellenberg indicator values for nutrients (N) and light (L).

To determine the set of traits out of the total set (table 1), which best described the variation in plant composition along the disturbance gradient and to be included in final analyses (Q-table), we applied the method of iterative RLQ-analysis as proposed by Bernhardt-Römermann *et al.* (2008). With this procedure traits were chosen based on their actual power to describe the variation of vegetation along the studied environmental gradient: iteratively, RLQ-analyses were performed with all possible sets of traits.

A final RLQ was carried out using the subset of traits which reached maximum correlation between the trait-environment model per axis resulting from the RLQ-ordination and the initial CA-ordination on the L-table (compare table 1). To detect functional groups responding to the management gradient, the resulting species scores were clustered by k-means clustering and cluster stability was examined using non-parametric bootstrapping following the methods described in Römermann et al. (2009).

Plant functional groups were characterized by calculating mean values for metric traits and by dominating trait attributes of categorical traits. We tested for significant differences between the clusters using Kruskal-Wallis H-test followed by pairwise Wilcoxon rank sum tests (with p-value adjustment method holm) for metric traits and with Chi^2-tests for categorical traits.

All calculations were performed with the R software Version 2.8.0 (R Development Core team 2004) using the libraries ade4 (Chessel *et al.* 2004), fpc (Hennig 2006) and vegan (Oksanen *et al.* 2007).

Table 1: Information included in the iterative RLQ-analysis. R-table: environmental parameters (sites x parameters), L-table: vegetation relevés (species x sites), Q-table (species x traits), variables chosen for final RLQ-analysis are written in bold. Data on lateral spread and budbank were extracted from CloPla3, data on phenology, emergence season and dormancy from BIOPOP, all other traits were extracted from the LEDA-database.

Table	Factor/trait	Scale
R	**Management regime**	Grazing
		Mowing
		Mulching twice per year
		Mulching once per year, late
		Mulching every 2. year
		Burning once per year
		Burning every 2. year
		Abandonment
	Weighted Ellenberg L	Metric
	Weighted Ellenberg N	Metric
	Weighted Ellenberg F	Metric
	Weighted Ellenberg R	Metric
	Cover moss layer	Metric
	Cover litter layer	Metric
	Height of moss layer	Metric
	Height of litter layer	Metric
L	**Eight vegetation relevées per management regime** á 2m x 2m , recorded in 2000	Schmidt scale (percentage cover values: 0.1, 0.5, 1, 2, 3, 5, 8, 10, 15, 20, 25, 30, 40, 50, 60, 70, 75, 80, 90, 100)
Q	**Canopy height**	Metric
	Leaf distribution	Rosette, semi-rosette, leaves distributed regularly
	SLA	Metric
	Seed mass	Metric
	Woodiness	Woody, semi-woody, non-woody
	Lateral spread	< 0.01 m, 0.01 - 0.25 m, >0.25 m
	Lifespan	Long (perennials), short (annuals + biennials)
	Legume	Legume, non-legume
	Growthform	Therophytes, chamaephytes, hemicryptophytes, geophytes
	Highest budbank-layer	Soil surface / 0-10cm above ground / > 10cm above ground
	Phenology	Vernal, aestival, partly-evergreen, evergreen
	Seed shedding start / end / duration	Metric
	Dormancy	Physiological, physiological non-deep, physical, no dormancy
	Emergence season	Spring, all year, autumn

Course of plant functional group adaptation to management changes

To investigate the development of the derived functional groups in differently managed plots over time, we tested whether they showed directional development at the respective treatments. We used the long-term dataset and assigned the species of these permanent plots, to the RLQ-generated plant functional groups. Most of the species appearing in the long-term dataset were also present in the dataset used for the RLQ and therefore got their functional group directly assigned to the RLQ-generated functional groups. Species not present in the RLQ dataset were assigned to one of the RLQ-generated functional groups with the help of a classification key which was generated based on the final trait-table and the functional group affiliation of the species therein. The classification tree was calculated with the R software using the library tree (Ripley 2009).

Next, per functional group, cover values of the species belonging to the different plant functional groups were summed up for each time step included in the long-term dataset and

adjusted to 100 % total cover to correct for differences in cover estimations due to changing originators.

To test for directional changes in functional group development we performed linear regressions with percentage cover of each plant functional group as dependent variable and years of recording as explanatory variable. We corrected the models for temporal autocorrelation applying a heteroscedasticity and autocorrelation consistent (HAC) covariance matrix estimation implemented in the library sandwich in R (Zeileis 2004).

Interrelations between the functional groups

To investigate whether cover development of different functional groups was interrelated, correlations between functional group covers were carried out for every management treatment and all available points in time using Pearson correlations.

Results

Extraction of plant functional groups

The trait combination extracted from the iterative RLQ analyses and subsequently used for the final RLQ included canopy height, leaf distribution, woodiness, legume/non-legume distinction, highest budbank layer and seedling emergence season (table 1).

The first axis of the RLQ-ordination reflected the light-nutrient gradient as indicated by high, significant correlation values of the indicator values with the first axis (figure 2). Relevés of different management regimes were separated mainly along the first axis, the second axis separated grazing and burning treatments from the mulching once per year and every second year regimes.

The cluster analyses gave four stable clusters (table 2), which significantly differed in the mean, respectively distribution, of the six traits included in the RLQ.

The first, “rosettes” abbreviated cluster contained small, non-woody rosette and semi-rosette species mostly with buds up to the soil surface or a height of maximum 10 cm above soil surface.

Species of the second group were non-woody, of medium height, had buds up to a height of more than 10 cm above soil-surface and leaves distributed regularly or were semi-rosettes. Notably many species germinated year-round. In the following this group will be called ”opportunists” as most species of this group lack a specific germination season and therefore may germinate whenever conditions become suitable for germination.

The third cluster comprised, besides some non-woody species, all woody species of the study-site and two semi-woody species. Most of them had regularly distributed leaves and were from medium height to tall. 80 % of the species of this group, which will be called "legumes"-group in the following text, were legumes.

The fourth cluster was characterised by tall species with regularly distributed leaves and buds >10 cm above soil surface. This set of traits implied competitive strength – therefore this group was named "competitors". Many species of this group germinated in spring.

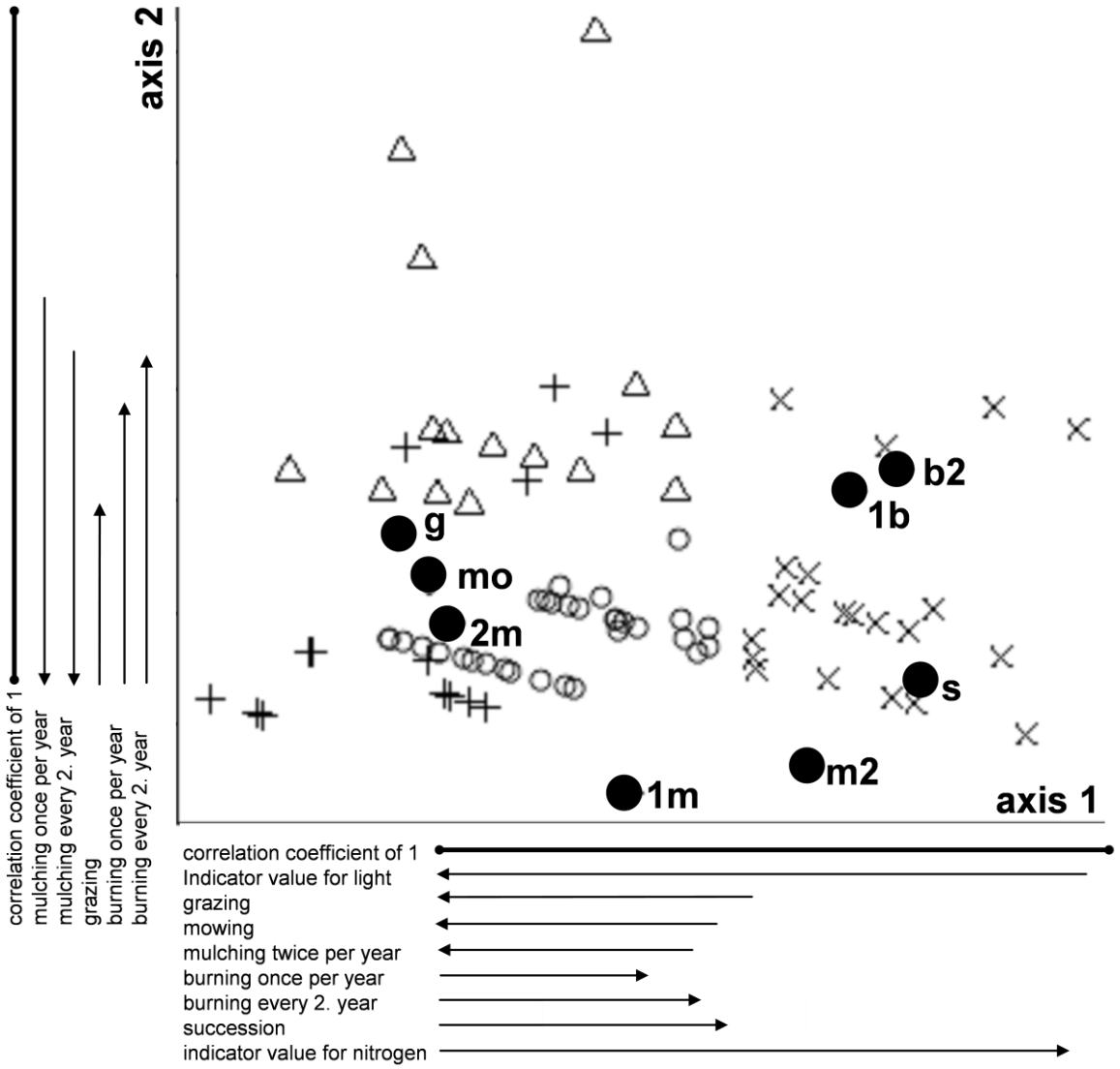

Figure 2: RLQ performed with vegetation relevés of the year 2000 (8 plots per management treatment). Diagram of plotted RLQ-scores for the vegetation relevés (large black circles= mean scores of all 8 plots per management treatment) and species (N=84). Species´ cluster affiliation is visualised by different symbols (+= cluster 1, o= cluster 2, ∆= cluster 3, x= cluster 4). Significant Pearson correlation coefficients of environmental parameters with the RLQ-axes are visualised by the length and direction of the arrows. The first arrow gives the length of r= 1 for calibration. g= grazing, mo= mowing once per year, 2m= mulching twice per year, 1m= mulching once per year, m2= mulching every 2. year, 1b= burning once per year, b2= burning every 2. year, s= succession.

Table 2: Characterisation of clusters obtained by k-means clustering of species scores of RLQ-analysis. Traits are shown which differed significantly ($p < 0.05$) between the species of the different clusters (Kruskal-Wallis H-test/Chi²-test) and three representative species per cluster are mentioned. For metric traits means and standard errors are listed, for nominal traits numbers of species belonging to each category are given below the categories.

	Cluster 1 "rosettes"	Cluster 2 "opportunists"	Cluster 3 "legumes"	Cluster 4 "competitors"
Canopy height	14.5 ± 2.4 cm *a*	26.1 ± 5.3 cm *b*	29.9 ± 3.4 cm *bc*	45.5 ± 2.4 cm *c*
Leaf distribution	Semi- / rosettes	Regularly/semi-/rosette	Regularly/semi-/rosette	Regularly/semirosettes
	4 : 10	12 : 19 : 0	13 : 2 : 2	22 : 2
Woodiness	Non-woody	Non-woody	Non-woody/semi-/woody	Non-woody/semiwoody
	14	31	4 : 2 : 9	21 : 3
Highest budbank-layer	Soil surface/0 - 10cm />10cm	> 10 cm	Soil surface/0 - 10cm/>10cm	0 - 10cm/>10cm
	8 : 4 : 2	31	1 : 2 : 12	1 : 23
Emergence season	Spring/autumn/all year	Spring/autumn/all year	Spring/autumn/all year	Spring/autumn/all year
	5 : 2 : 7	2 : 5 : 24	2 : 1 : 12	13 : 4 : 7
Legumes : non legumes	0 : 14	0 : 31	12 : 3	0 : 24
Representative species	*Carex caryophyllea*	*Asperula cynanchica*	*Hippocrepis comosa*	*Brachypodium pinnatum*
	Leontodon hispidus	*Cerastium arvense*	*Lathyrus pratensis*	*Centaurea jacea*
	Plantago media	*Leucanthemum vulgare*	*Lotus corniculatus*	*Galium aparine*
	Primula veris	*Sanguisorba minor*	*Teucrium chamaedrys*	*Hypericum perforatum*
	Viola hirta	*Poa pratensis*	*Vicia angustifolia*	*Koeleria pyramidata*

Course of plant functional group adaptation to management changes

We used the long-term data set to investigate the development of the functional groups during the last 30 years (figure 3A-H shows graphically the development of each of the four functional groups at each of the management treatments; in table 3 the results of the linear regressions are given). As shown in figure 3A the traditional grazing treatment maintained the functional group composition present at the beginning of the experiment in 1975 to a large extent. Despite shifts in functional group composition no trend could be found for any group to decline or increase. The lowest divergences to the original functional group composition were found at the mowing treatment and at the mulching twice per year treatment (figure 3B and C). At the mowing treatment only the “legumes”-group showed a significant upward trend. At the mulching twice per year treatment the “competitor”-group was the only group with a significant trend to increase. All other treatments (figure 3D-H) led to more pronounced changes from the original functional group composition. Especially the group of the competitive species significantly increased in all other treatments. Species of the ”rosettes”-group significantly increased at the mulching once per year treatment and decreased at mulching every second year, at the burning every second year treatment and at succession. The “opportunists”-group decreased in the same treatments in which the “rosettes”-group decreased significantly plus at burning once per year. Unlike reacted the “legumes”-group which only declined significantly at the treatments burning once per year and mulching once per year, while it had an upward trend at the mowing treatment.

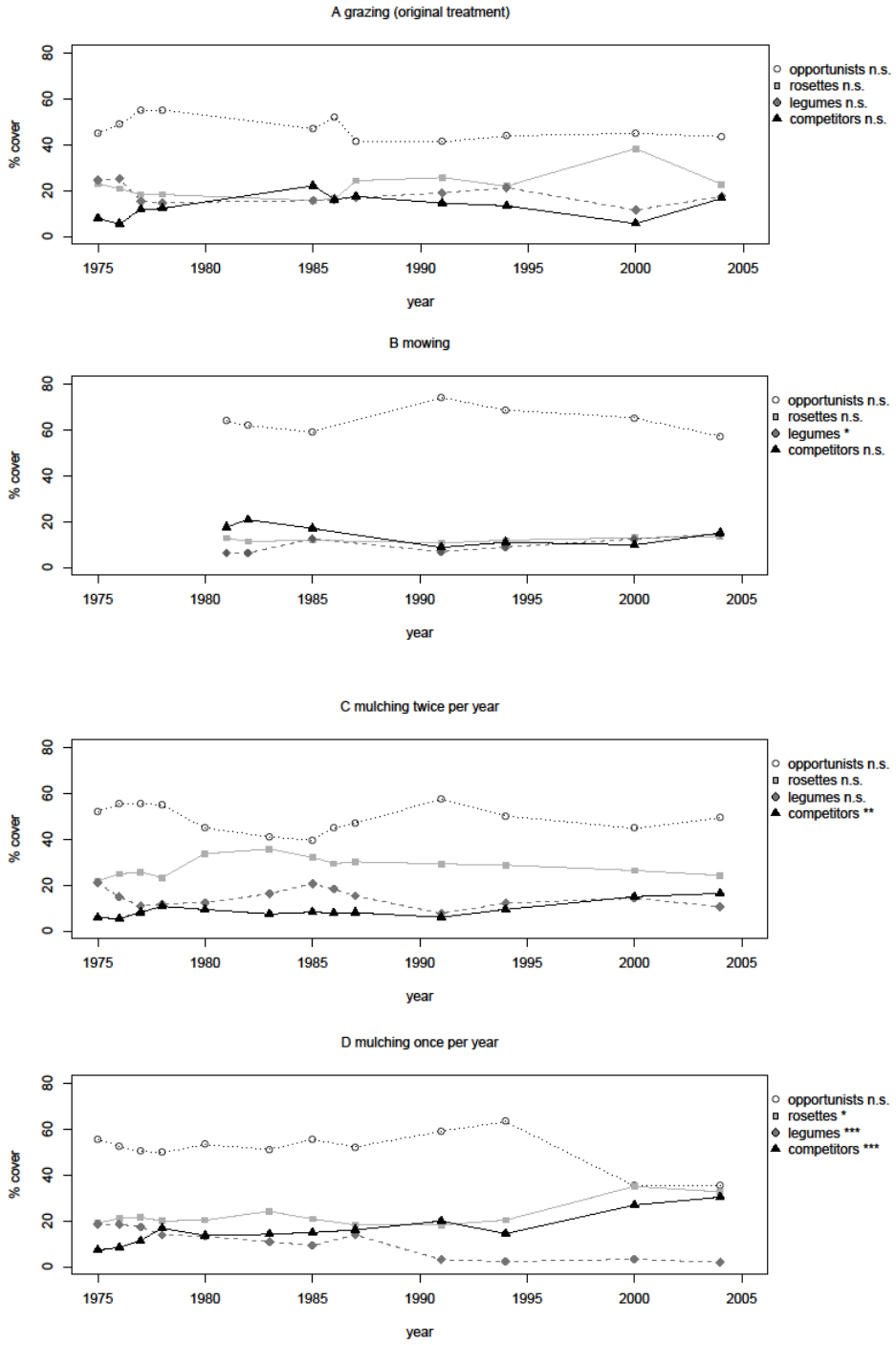

Figure 3: Assignment of species recorded in long-term vegetation data of the same study site to the RLQ generated groups. Summed up cover values of species belonging to the four functional groups are displayed for each time step. Cover values of each time step were adjusted to 100 % total cover to correct for differences in cover estimations due to changing originators. Significance of the models: ***p<0.001, **p<0.01, *p<0.05, n.s. not significant.
Detailed information on the linear regression models is given in table 3.

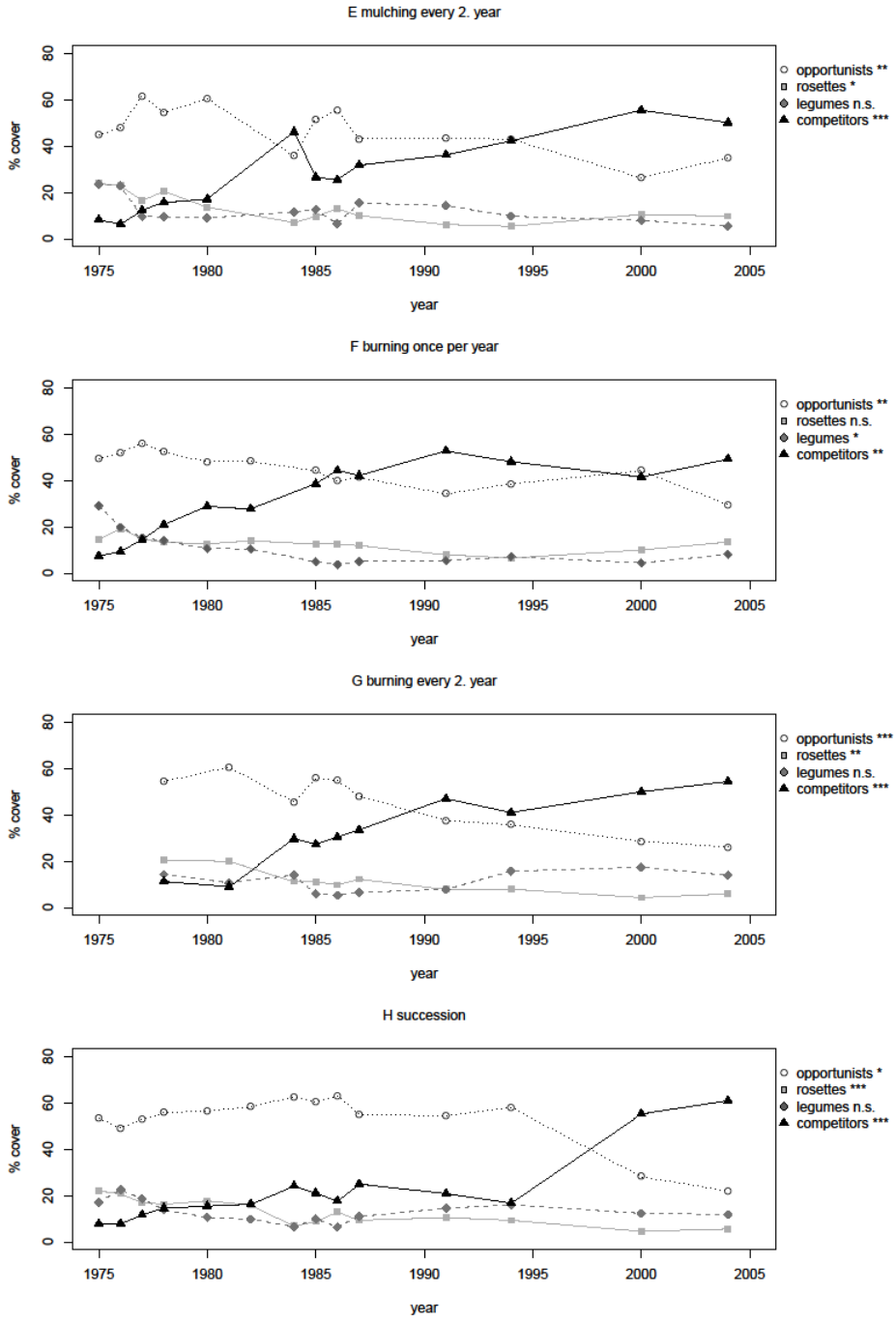

Figure 3: continued.

Table 3: Information on the regression models for functional group cover development over time. p-values were corrected for temporal autocorrelation.*p<0.001, **p<0.01, *p<0.05, n.s. not significant.**

		Estimates	± Standard error	r	p- value	
Grazing	Opportunists	-0.29	± 0.14	-0.58	0.065	n.s.
	Rosettes	0.33	± 0.17	0.54	0.083	n.s.
	Legumes	-0.16	± 0.14	-0.39	0.265	n.s.
	Competitors	0.12	± 0.17	0.23	0.487	n.s.
Mowing	Opportunists	-0.03	± 0.24	-0.04	0.918	n.s.
	Rosettes	0.05	± 0.04	0.48	0.234	n.s.
	Legumes	0.28	± 0.08	0.73	0.016	*
	Competitors	-0.31	± 0.18	-0.61	0.137	n.s.
Mulching	Opportunists	-0.15	± 0.15	-0.23	0.353	n.s.
twice per year	Rosettes	0.02	± 0.16	0.05	0.893	n.s.
	Legumes	-0.14	± 0.09	-0.33	0.154	n.s.
	Competitors	0.27	± 0.07	0.74	0.004	**
Mulching	Opportunists	-0.42	± 0.28	-0.49	0.173	n.s.
once per year	Rosettes	0.40	± 0.14	0.70	0.016	*
	Legumes	-0.61	± 0.07	-0.92	0.000	***
	Competitors	0.63	± 0.1	0.90	0.000	***
Mulching	Opportunists	-0.79	± 0.21	-0.70	0.003	**
every 2. year	Rosettes	-0.48	± 0.19	-0.72	0.026	*
	Legumes	-0.35	± 0.17	-0.57	0.064	n.s.
	Competitors	1.62	± 0.18	0.91	0.000	***
Burning	Opportunists	-0.69	± 0.16	-0.83	0.001	**
once per year	Rosettes	-0.20	± 0.1	-0.60	0.080	n.s.
	Legumes	-0.53	± 0.23	-0.67	0.044	*
	Competitors	1.42	± 0.37	0.84	0.003	**
Burning	Opportunists	-1.36	± 0.12	-0.93	0.000	***
every 2. year	Rosettes	-0.57	± 0.14	-0.87	0.004	**
	Legumes	0.21	± 0.17	0.39	0.258	n.s.
	Competitors	1.71	± 0.24	0.93	0.000	***
Succession	Opportunists	-0.89	± 0.4	-0.65	0.049	*
	Rosettes	-0.54	± 0.08	-0.86	0.000	***
	Legumes	-0.15	± 0.17	-0.30	0.386	n.s.
	Competitors	1.58	± 0.32	0.88	0.000	***

Interrelations between the functional groups

No significant correlations between the relative cover of functional groups were found at the grazing and at the mowing treatment (table 4). However, at all other treatments several significant correlations were detected. Most striking was that except at the grazing, mowing and the mulching twice per year treatment gain in cover of the competitive species was significantly negative correlated with the cover of the "opportunists"-group which dominated at the grazing treatment.

Table 4: Cross-correlation between the relative cover of functional groups for each management regime including all available years of the long-term vegetation dataset. Pearson correlation coefficients are shown with ***p<0.001, **p<0.01, *p<0.05, n.s. not significant

		Opportunists	Rosettes	Competitors
Grazing	Legumes	-0.26 n.s.	-0.22 n.s.	-0.30 n.s.
	Opportunists		-0.52 n.s.	-0.14 n.s.
	Rosettes			-0.52 n.s.
Mowing	Legumes	-0.57 n.s.	0.61 n.s.	-0.17 n.s.
	Opportunists		-0.63 n.s.	-0.70 n.s.
	Rosettes			0.12 n.s.
Mulching twice per year	Legumes	-0.57*	-0.08 n.s.	0.30 n.s.
	Opportunists		-0.67*	-0.22 n.s.
	Rosettes			0.19 n.s.
Mulching once per year	Legumes	0.23 n.s.	-0.52 n.s.	-0.80**
	Opportunists		-0.89***	-0.71**
	Rosettes			0.77**
Mulching every 2. year	Legumes	-0.01 n.s.	0.54 n.s.	-0.55*
	Opportunists		0.41 n.s.	-0.79**
	Rosettes			-0.82***
Burning every year	Legumes	0.60*	0.60*	-0.88***
	Opportunists		0.58*	-0.89***
	Rosettes			-0.77**
Burning every 2. year	Legumes	-0.57 n.s.	-0.15 n.s.	-0.22 n.s.
	Opportunists		0.82**	-0.91***
	Rosettes			-0.96***
Succession	Legumes	-0.20 n.s.	0.52 n.s.	-0.32 n.s.
	Opportunists		0.37 n.s.	-0.83***
	Rosettes			-0.78***

Discussion

Definition and characterization of plant functional groups

In the first step of our study we were able to extract plant functional groups based on the set of traits that best explained differences in plant species composition and environment at different management treatments. The six traits, which turned out to be functional for the studied land-use-gradient, covered traits mainly important for the competitive ability and persistence of plants (canopy height, leaf-distribution, legume/non-legume and woodiness), one trait reflecting the regeneration potential (highest budbank-layer) and one germination related trait, the germination season. The importance of height and leaf-distribution for plant performance under different management regimes is stressed in many studies (e.g. Ellenberg 1952; Noble & Slatyer 1980; Díaz & Cabido 2001; Hellström *et al.* 2003; Garnier *et al.* 2007). Vertical distribution of buds determines the resprouting potential after different kinds

of disturbances (Vesk & Westoby 2004; Vesk *et al.* 2004b). Since plants generally resprout from buds closest to the tissue lost at a disturbance event (Bellingham & Sparrow 2000), high buds should enable the plant to reoccupy space soon after above-ground disturbances and therewith to retain their competitive strength. The inclusion of the emergence season indicates that the differences in seasonal timing and frequency of gap formation at the different management regimes lead to a selection of species already at the stage of germination (Olff *et al.* 1994; Schütz 2000; Kahmen & Poschlod 2008b).

The trait combination used for our functional group definition shows, that for the functional analysis of the studied land-use gradient it would have been inappropriate to group species without considering traits linked to competitive ability as well as to regeneration ability and germination niche. By the used method of functional group definition it was possible to determine the most appropriate trait set and subsequently to derive useful functional groups.

Four functional groups were determined which reacted to the eight management treatments and accompanying environmental conditions in different ways.

The first, "rosettes" abbreviated cluster, comprised small, non-woody rosette and semi-rosette species mostly with highest buds located at the soil surface. Small rosette species are poor competitors and often restricted to unproductive or disturbed sites where competition is low (Grime 1979). Many species of this group, like *Viola hirta*, *Carex caryophyllea* or *Bellis perennis*, start seed-shedding early in the season which can be interpreted as strategy to escape competition and reduced seed dispersal distances later in the season, when surrounding vegetation is high (Clements 1928; Kunzmann 2000).

The second group was called "opportunists"-group as most species of this group lack a specific germination season and therefore may germinate whenever conditions become suitable for germination. Delayed germination is typical for species which depend on gaps created during the growing season for their germination (Schütz 2000). Species of this group were typically non-woody, medium high semi-rosettes with good resprouting ability after disturbance. This set of trait attributes reflects known adaptations of plants to grazing (Díaz *et al.* 1992; Díaz *et al.* 2007).

The third group ("legumes") comprised, besides three non-legume species, all legumes of the study site. Especially at the treatments with lower nutrient availability, like grazing or mowing, the legumes of this group might profit from nitrogen fixation-ability. Woodiness is further characteristic for this group: all woody species of the study-site and two semi-woody species belonged to this group. Competitive strength of this group is also indicated by the

prevailing regularly distribution of leaves and a medium-high to tall stature in comparison to the other groups.

The fourth cluster was characterised by large, non-woody, but also some semi-woody, species with regularly distributed leaves and good resprouting ability. Tall stature and leaves high in the canopy are advantageous when disturbance frequency is low (Grime 1979). Thus this trait combination describes highly competitive species, typical for later successional stages (Kahmen & Poschlod 2004).

Based on this knowledge of the strategies displayed by the four functional groups, the mechanisms of changes in functional group composition in adaptation to a new management regime became clearer.

Development of plant functional group composition over time

Mechanisms behind species changes became visible when the cover of the functional groups was plotted against the time gradient. The traditional management grazing showed pronounced fluctuations of the covers of all functional groups between the different recording years. Those fluctuations may be due to year to year differences in grazing times and intensities. The important point is that none of the functional groups consistently declined or increased over time. This indicates that vegetation is in equilibrium on this historically managed site (compare also Römermann *et al.* 2009).

Mowing once per year seemed to be the best surrogate for the traditional grazing treatment in this study as it was the only treatment where the "competitors"-group cover did not increase at the expense of other groups over time. Fluctuations in the cover of functional groups were much smaller at the mowing treatment than at the grazing treatment. Grazing animals affect plant communities through their impact on dominant species, propagule transport and plant regeneration opportunities on bare ground created by small-scale disturbances (Crawley 1997; Olff & Ritchie 1998). However, the extent of these grazing effects may differ from year to year due to variability in intensity, timing and duration of grazing. Thus larger fluctuations in functional group may be due to the higher controllability of mowing effects on the vegetation in comparison to grazing. That annual mowing is most likely capable to sustain plant composition and thus functional group composition of formerly grazed sites has been shown by several authors (Ryser *et al.* 1995; Huhta *et al.* 2001; Römermann *et al.* 2009). The only increasing group at the mowing treatment was the „legumes"-group. As this group should benefit the more the lower nitrogen availability at a treatment is (Tilman 1986), the success of this group at the mowing treatment with regular biomass removal was not surprising. The

importance of the ability to improve nutrient uptake at treatments leading to nutrient impoverishment compared to treatments leading to enrichment (like succession or mulching regimes) has also been shown for mycorrhization degrees (Bernhardt-Römermann *et al.* 2009).

Our results suggest that at all other treatments except the grazing and mowing treatment the increase of one group occurred at the expense of one or several other functional groups. Here, the significant increase of the "competitors"-group was striking. The enhancement of the competitive species may be attributed to auteutrophication and/or accumulated input of atmospheric nitrogen. Auteutrophication at mulching treatments has been reported for semi-natural grasslands (Bakker 1989; Briemle 2005) and atmospheric nitrogen deposition is a common problem all over Europe (Stevens *et al.* 2004; Bobbink & Roelofs 2005). In contrast to this finding, grazing proved to be able to counter negative effects of N-input (Jacquemyn *et al.* 2003a) - most likely because of the creation of competition-free gaps despite raised productivity. But also the non-fertilized mowing regime may counter effects of nitrogen-input by regularly removing biomass and with it nutrients. However as Wilson et al (1995) stated, the impact of management on community composition is much more pronounced compared to the N-deposition. Therefore the gain in cover of the "competitors"-group at most treatments after management change should be credited to the end of selective suppression of these tall species. Since the balanced functional group composition of the grazing treatment can only be maintained and competitive exclusion prevented when potentially dominants are restrained by management and harmed by high biomass loss (Klimes & Klimešová 2002). The "opportunists"-group was most evidently negatively affected by the increasing dominance of the "competitors"-group. These are not only well adapted to disturbances created by grazing, but are also dependent on these disturbances for regeneration and weakened when competitive species can display their full competitive strength.

Besides the importance of the "competitors"-group for changes in functional group composition, further management dependent changes could be observed: the "rosettes"-group was promoted by the mulching once per year treatment and declined significantly at the mulched every second year field, the burned every second year and abandoned fields. The outstanding role of light availability as the main mechanism for diversity loss and recruitment failure of small plants in the understory due to higher productivity after eutrophication was demonstrated by Hautier *et al.* (2009). Hence due to their low stature species of the "rosettes"-group seemed to be dependent on the low sward after winter to be able to recruit, flower and set seeds before surrounding vegetation shortens the light supply.

The “legume”-group showed fewest significant reactions to changed management treatments. This group only increased at the mowing treatment and declined significantly at the once per year burned and once per year mulched field. At these fields the decline of this group was negatively correlated with the cover development of the competitive species. Hence, although species of the “legume”-group may have been suppressed by the “competitors”-group at least at some treatments, they were less negatively affected by management changes than the “rosettes”-group or the “opportunists”-group. Since species of the “legume”-group mainly have regularly distributed leaves and a mean height lower but not significantly different from species of the “competitive”-group, this group could be expected to be competitive strong as well. Furthermore the ability of most of the species of this group to fix nitrogen and woodiness may attribute to competitive strength. The decline of the “legume”-group at the burning once per year treatment was contradictory to the promotion of woody species at burned grasslands as reported by (Briemle 1991). He suggested that for nanophanerophytes the advantage of reduced competition after a fire event may level out the negative effects of fire damage. Further, promotion of legumes at annually burned grasslands could be expected due to increased nitrogen limitation at frequently burned sites (Vitousek & Howarth 1991; Hendricks & Boring 1999).

Overall, the pattern of plant functional group development at the different management regimes and especially the obvious suppressing impact of the “competitive”-group on the other groups, imply that not only the potential plant species diversity declines with the intensity of competition (Grime 1979, 2006) but also the functional group diversity of a community.

Striking is also the result, that even after 30 years the adaptation of the plant communities to the altered management regime has not reached a new stable state concerning functional group composition (compare also results in Römermann *et al.* 2009). The significant correlations of functional group covers over time indicated a response of these groups to management induced changes in abiotic conditions and biotic interactions. Thus cover changes of these functional groups went beyond year and weather dependent fluctuations in species composition, which also occur at each community in equilibrium (Grubb 1977). Major changes in plant functional group composition occurred in the last ten years included in this study. Our results suggest that at all treatments, except grazing and mowing, the group of competitive species may further increase in cover and thus may lead to ongoing cover losses of species belonging to other functional groups. It has been noted by several authors that it can take decades for grasslands to adapt to changed environmental conditions (Ellenberg

1952; Pakeman *et al.* 2002; Vanderpoorten *et al.* 2004). This indicates that predictions of changes in plant composition due to management changes, based on results of short term studies, should be taken with caution. Further, ongoing changes in functional group composition may lead to total exclusion of single functional groups. At the abandoned field as well as at all mulching and burning treatments a new equilibrium is not reached and exclusion of functional groups may simply be postponed.

Generalization and transferability of the results

Plant functional trait studies often indicated some limitation of their applicability over a broad range of environments and species pools (Pakeman 2004; Vesk *et al.* 2004a; de Bello *et al.* 2005; Díaz *et al.* 2007). They concluded that the relevance of single traits might depend on environmental conditions or historical background of management regimes (Díaz *et al.* 2007). The number of functional groups is unlimited and dependent on the specific question (Körner 1993; Wright *et al.* 2006). Thus functional groups defined for one study might have limited use under different environmental conditions etc. (Weiher *et al.* 1998).

The current study should be taken as a contribution to a better understanding of ecosystem processes in reaction to disturbance by certain management practices. The homogeneous vegetation at all management fields at our study site at the onset of the different management regimes was crucial for our approach and for demonstrating the mechanisms behind species changes.

Conclusions

With our approach we succeeded to determine plant functional traits and subsequently groups that differ in importance at the tested management treatments. When the functional group composition was plotted against time it became clear that these groups display the driving forces of changing species composition. Dependent on management treatment discrete functional groups showed significant trends over time and thus clearly reacted to single management treatments. Based on development of functional group partition over time, functional mechanisms behind the obvious changes in plant species composition were revealed.

Chapter 3

Winner and loser plants in differently managed grasslands: a trait-based approach

Abstract

One way to study assembly processes of plant communities is the analysis of long-term vegetation datasets. Here we focused on plant extinctions and invasions in differently managed grasslands over the time span of more than 30 years. First, we asked if different management treatments (grazing, mulching twice per year, mulching once per year, burning once per year and abandonment) differed with regard to invasibility or plant extinction numbers. Secondly, we performed a pooled analyses and a meta-analysis over six sites per management treatment contrasting invader and extinct species´ traits to find management dependent effects of trait selections.

The different management treatments did not differ in invasion rates. This could originate either from seed limitation, from very low establishment success at all management treatments or a combination of both factors. In contrast, extinction rates differed significantly between the treatments. Extinction rates increased from grazing, mulching twice, mulching once and burning to abandonment. The mean number of invasions exceeded the number of extinctions only at grazing, while that relation was reversed at the other management treatments.

Accordingly, the trait based analyses showed that least trait selection occurred at the grazing treatments and at mulching twice per year, while strongest trait selection pressures acted at abandonment. Management specific trait selection patterns could be revealed, e.g. the selection for higher seed masses reached the highest effect size at mulching once per year - most probably due to the dense litter layer – while burning favoured the invasion of species with lower Ellenberg values for moisture and nutrients. Furthermore, the meta-analysis indicated that at all management treatments invaders tended to be more competitive than extinct species.

Only at grazing and mulching twice per year trait selection pressures were low what resulted in low species extinction numbers. At these two managements extinct and invading species were almost a random draw from the species pools and therewith only these managements

should allow to maintain not only high species diversity but also high functional diversity in the long run.

Introduction

Traditional grasslands with their unique species sets are products of centuries or even millennia of human activity (mowing or grazing initially combined with clearing) and have long been prominent features of the man-made landscapes in central Europe. Many of them already got lost by fertilization, abandonment or afforestration during the last century (Poschlod & Schumacher 1998; WallisDeVries *et al.* 2002). Due to their high species diversity and rare plants occurrences, remnants of traditionally managed grasslands are of major conservation value today. Though many studies on different management treatments concluded that the best way to maintain the plant species and functional group composition of semi-natural grasslands is to reintroduce the traditional management treatments grazing or mowing (Bobbink & Willems 1993; Kahmen *et al.* 2002; Moog *et al.* 2002; Römermann *et al.* 2009), those recommendations are rarely realized for economic as well as for organizational reasons.

Therefore, different management treatments have been tested as alternatives to the traditional grazing or mowing treatments to maintain species and functional trait diversity over different grassland types in southwest Germany for over 30 years until today. These alternative treatments include burning and mulching treatments but also abandonment.

Changing management or abandonment alter species assembly processes by changing resource availabilities, abiotic conditions and competitive or facilitative interactions (Mayfield *et al.* 2005). The impact of management change on assembly processes can be visualized by following changes in plant species number and in plant functional trait composition.

Changes in species number provide information on invasibility and on the strength of selection pressures exerted by the different management treatments.

The usage of plant functional traits provides the opportunity to filter out trait selections based on management induced changes of assembly processes and therewith to make universal predictions on the consequences of land-use changes (Lavorel & Garnier 2002; Pakeman *et al.* 2008). It has been shown in previous studies that land use regimes may be defined as specific disturbance regimes which act as filters on functional trait distributions (Díaz *et al.* 1992; Dupré & Diekmann 2001; Pakeman 2004). Abandonment as well promotes certain trait attributes over a wide range of grassland types (Kahmen & Poschlod 2004).

Identifying traits that divide winner from loser plant species at different management treatments could help to unravel the mechanism(s) that drive species changes.

Two processes linked to management changes are in the focus of the current study: (1) changed invasibility and species extinction rates after management changes and (2) functional trait selections exerted by different management treatments.

For the assessment of management suitability we presume that high species and functional diversity can be maintained when species losses at least do not exceed invasions and if extinctions and invasions are randomly distributed across functional trait groups.

We decided for the comparison between extinct and invaded species rather than between decreasing and increasing species as traits that facilitate a species´ presence may not coincide with those that determine a species´ ability of becoming abundant (Grubb 1986; Cingolani *et al.* 2007). Furthermore, contrasting extinct and invaded species´ traits against constant species traits may hide trait selection pressures after management change. This should be the case when constant species just did not react during the time frame of the study. Numerous studies have shown that inertia of vegetation after environmental change can lead to quite stable species compositions over decades even though actual environmental conditions prevent successful generative regeneration of these species.

We tested the hypothesis that the trait values represented among extinct and invaded species were a random draw from the species pool. We tested the consistency of functional trait selection caused by different management treatments over six study sites.

Therewith, the aim of this study was to address the following questions:

(1) Do different grassland managements differ in their invasibility or number of extinctions?

(2) Dependent on the respective management treatment: do the traits of invaded and extinct species differ? What are the acting selection pressures at the different management regimes?

Material and methods

Data sets

Long-term vegetation datasets from the "Fallow experiments Baden-Württemberg" were analysed. For these experiments several former meadows and pastures in southwest Germany were split into fields lying next to each other and consequently subjected to one management treatment each since 1975 (Schreiber *et al.* 2009). An overview over the analysed study sites

and management treatments is given in table 5 and table 6. Different kinds of grasslands were included to filter out overall effects of the different management treatments on plant functional trait selection.

The applied management treatments include grazing, different mulching regimes (mulching twice per year and once per year), burning in winter each year and abandonment. Permanent plots of 5 m x 5 m were installed at the beginning of the experiment and recorded regularly until 2008 (Schreiber *et al.* 2009).

The datasets comprise vegetation records of these permanent plots from 1975 to 2008. For our analyses we focused on study sites, at which the same set of management treatments was applied including at least mulching twice and once per year, burning once per year and abandonment.

Grazing is the original management treatment of most of the study sites and proved to maintain species richness most successfully in former studies. Therefore, it was indicated to include this treatment in the analysis as reference treatment. Nevertheless, grazing was not applied on each study site of the fallow experiments. Hence, further sites were included on which only vegetation development under grazing was monitored since 1975.

We first carried out broad analyses on a pooled data set and subsequently performed a meta-analysis of the individual study sites.

For all functional trait analyses we concentrated on the herbaceous species only. Including traits of shrubs and trees would have hampered to find patterns of trait selection.

Table 5: Characterisation of the 10 study sites. Altitude (m a.s.l.), precipitation (mm/year), mean annual temperature (°C), geology and Ellenberg (2001) indicator values of soil reaction (pH) and nitrogen (N), calculated from the vegetation relevés in 1976. Vegetation types are taken from Schiefer (1981), nomenclature of vegetation types according to Rennwald (2000).

study site	m.a.s.l.	mm/year	°C	geology	pH	N	initial vegetation
Ettenheim	290	900	8.5	sandstone	6.5	5.8	Arrhenatherum elatioris BRAUN 1915
Fischweiher	220	950	8.5	raw warp	4.3	3.9	Angelico-Cirsietum oleracei Tx. 1937
Oberstetten	380	700	9.0	limestone	7.7	4.1	Arrhenatherum elatioris BRAUN 1915
Rangendingen	460	750	8.0	gypsum	7.2	3.4	Brometum Scherrer 1925
St Johann	760	1000	6.5	limestone	7.3	2.5	Gentiano-Koelerietum pyramidatae Knapp ex Bornkamm 1960
Bernau	1100	1800	5.5	sandstone	2.2	2.9	Festuco-Genistelletum sagittalis Issler 1929
Schönau	730	1600	7.0	granite	4.5	2.6	Arrhenatherum elatioris BRAUN 1915
Schopfloch	730	1000	7.0	limestone	5.4	5.0	Lolio perennis-Cynosuretum cristati Tx. 1937
Fröhnd	840	1800	6.0	gneiss	3.3	2.4	Festuco-Genistelletum sagittalis Issler 1929
Hepsisau	560	900	8.0	limestone	6.9	6.2	Arrhenatherum elatioris BRAUN 1915

Table 6: Sites and management treatments included in the analyses.

study site	grazing	grazer	mulching twice	mulching once	burning once	abandonment
Ettenheim			x	x	x	x
Fischweiher			x	x	x	x
Oberstetten			x	x	x	x
Rangendingen			x	x	x	x
St Johann	x	sheep	x	x	x	x
Bernau	x	cattle	x	x	x	x
Schönau	x	sheep, cattle				
Schopfloch	x	sheep				
Fröhnd	x	cattle				
Hepsisau	x	sheep				

Invasions and extinctions at different management treatments

For our analyses we used the vegetation relevés from the first and from the last recorded year and filtered out the species belonging to the invader and to the extinct species group.

The first group "extinct species" comprised species that were present at the onset of the new management treatments but went locally extinct and thus were not recorded at least at the last census in 2008. The second group consisted of the "invaders". Those were recorded in 2008 but not at the onset of the new management.

To test if the different management treatments differed in invasibility and extinctions we calculated ratios from invaded and extinct species numbers relative to the number of species in the initial species sets to take into account the different species pool sizes at the different study sites.

Furthermore, we calculated the ratios of number of extinctions/number of invasions to visualize species pool size independent values of species diversity decline or increase at the different managements over the different study sites.

We tested for management dependent differences of these ratios applying ANOVA followed by post-hoc LSD-tests. Assumptions on normal distribution and homogeneity of variances were tested and met for these data sets.

Plant traits

For all species included in the vegetation records, we collected information on functional traits which were extracted from the databases LEDA (Knevel *et al.* 2003, www.leda-traitbase.org; Kleyer *et al.* 2008), BIOPOP (Jackel *et al.* 2006, www.floraweb.de/proxy/biopop/de/index.php), Electronic Comparative Plant Ecology ("ECPE", Grime *et al.* 1988; Hodgson *et al.* 1995) and CloPla3 (Klimešová & de Bello 2009,

http://clopla.butbn.cas.cz) (table 7). Besides these basic traits we included the Ellenberg indicator values (Ellenberg *et al.* 2001), the non-legume/legume distinction and the herb/grass distinction.

Based on a previous analysis on plant functional groups that differed in importance at different management treatments at one site of the "Fallow experiments", species were also assigned to these functional groups (see chapter 2 for the description of the functional groups).

Not all traits were available for all species (table 7).

Table 7: Plant functional traits and classifications included in the analyses. Trait units, data sources and percentage of missing values are given. Data sources: LEDA (Kleyer *et al.* 2008), BIOPOP (Jackel *et al.* 2006), ECPE= Electronic Comparative Plant Ecology (Hodgson *et al.* 1995), CloPla3 (Klimešová & Klimes 2008; Klimešová & de Bello 2009), Ellenberg indicator values (Ellenberg *et al.* 2001).

	unit	data source	% missing values
seed mass	[mg]	LEDA	4
seedbank longevity index	0-1	LEDA	3
emergence season	spring, autumn, all year	BIOPOP	5
min. germination temperature	°C	BIOPOP	50
light requirement for germination	light > darkness, darkness ≥ light	BIOPOP	50
dormancy	no dormancy, physiological dormancy, physical dormancy	BIOPOP	19
canopy height	[m]	LEDA	0
SLA	[mm²/mg]	LEDA	1
vegetative lateral spread	very small (therophytes), <100mm, 100-250 mm, >250 mm per year	ECPE / CLOPLA3	4
leaf distribution	regularly, semi-rosette, rosette	LEDA	0
legume	yes, no	-	0
woodiness	woody, semi-woody, non-woody	LEDA	0
grass	yes, no	-	0
minimum bud bank depth	soil-surface, 0 -10 cm, >10 cm	LEDA	5
seed shedding earliest month	1 (january) - 12 (december)	LEDA	7
seed shedding latest month	1 (january) - 12 (december)	LEDA	7
seed shedding duration	1 (january) - 12 (december)	LEDA	7
Ellenberg N	1 - 9	Ellenberg	13
Ellenberg F	1 - 9	Ellenberg	30
Ellenberg L	1 - 9	Ellenberg	2
functional group	"competitor", "rosette", "legume", "opportunist"	chapter 2	6

Pooled analyses

Species were pooled across the study sites into two groups. The first group "extinct species" comprised species that were present at the onset of the new management treatments but were not recorded at the last census in 2008. The second group consisted of the "invaders". Those were recorded in 2008 but not at the onset of the new management.

In preliminary analyses the differences between invaders and extinct species promised to reveal more about trait selection mechanisms than comparing extinct and invaded species with constant species, which were present from the beginning of the experiments until the last census. Especially grasses were overrepresented in the constant species group in comparison

to the invaded and extinct species groups at all managements (tested with Chi^2-statistics). Furthermore, invaded and extinct species may better represent actual selection pressures than constant species, which may have persisted due to inertia of vegetation after management changes and not necessarily due to best adaptation to the new management treatment.

Metric traits were tested with Mann-Whitney U-tests for significant differences between the extinct species group and the invaded species group, as assumptions for parametric testing were not met.

For categorical traits contingency tables were used and the likelihood ratio statistic was calculated (Agresti 1996). Adjusted residuals were used to indicate over- or underrepresentation in cells, for which absolute values greater than about 2 are noteworthy (Agresti 1996). Analyses on the pooled data set were performed using SPSS for Windows 17.0.

However, if species occurred at more than one study site they were counted several times and therewith inflated the sample size. Additionally, a species and its trait value could potentially be represented in each of the two groups when it occurred at several sites at the same management treatment.

Furthermore, site specific differences with regard to climate, soils or vegetation may obscure consistent trait selection patterns over the different study sites.

Nevertheless, the advantage of the pooled analysis was its simplicity and large sample size.

Meta-analyses

As species could have conflicting responses in different studies, we also performed a meta-analysis. This allowed determination of relationships between traits and the likelihood of one of two responses for each study site in a consistent, comparable manner. In these analyses, each study site was analysed separately to determine size of the effect that a particular trait or trait attribute had on the probability of a species being in the group of extinct or invaded species. We calculated effect sizes for differences between extinct species and invaded species.

To compare the size of effect that traits had for selection between extinct and invaded species we calculated Hedges d. Although the effects are measured with different units the metric used to calculate Hedges d standardizes them to a single scale. Hedges d is an estimate of the standardized mean difference that is not biased by small sample sizes (Hedges & Olkin 1985). The highest effect sizes are from those study sites showing large differences between the groups and low variability. Positive d values imply that the possession of a trait attribute or

high values of continuous traits increase the probability to become extinct or to invade at the respective management treatment. Hedges d was weighted by an estimate of precision of the effect size, based on the assumption that studies with larger sample size should be weighted more heavily than those that are less precise. Also dependence on parametric assumptions was decreased by using the weighting w= Nin*Nex/(Nin+Nex) (Hedges & Olkin 1985) where Nin is the species number of invaded species and Nex the number of the extinct species. The conventional interpretation is that an effect size of 0.2, 0.5 and 0.8 indicate small, medium and large effect sizes, respectively (Cohen 1969).
Categorical variables were transformed to dummy variables for the meta-analysis.
Hedges d was calculated in Excel.

Results

Invasions and extinctions at different management treatments

The different management treatments did not differ in new species invasion rates (figure 4A).
In contrast, extinction rates differed significantly between the treatments (figure 4B). The extinction rate increased from grazing, mulching twice, mulching once, burning once per year to abandonment.
The mean number of invasions exceeded the number of extinctions only at the grazing treatment, while that relation was reversed at the other management treatments (figure 4C). However, significantly higher ratios from extinct to invaded species numbers were only reached for abandonment.

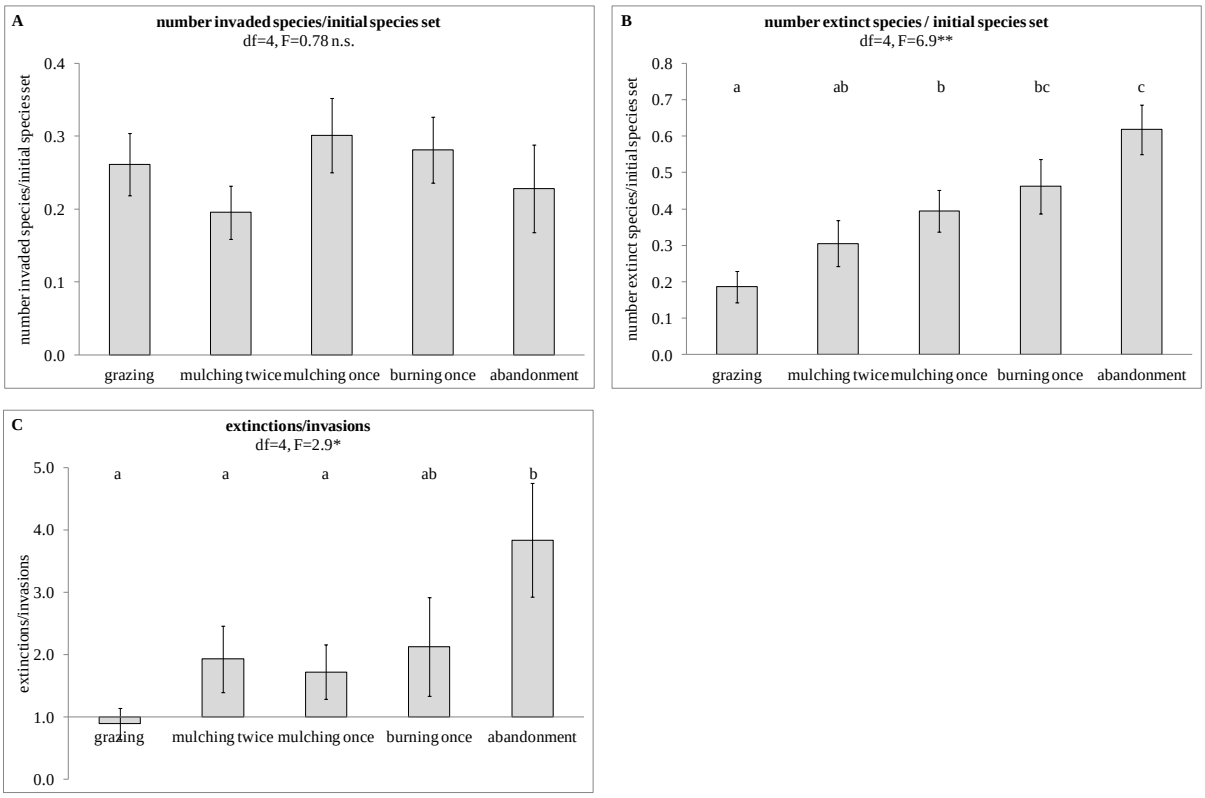

Figure 4: Number of invaded (A) and extinct species (B) relative to the initial species sets and ratio of number of extinctions to number of invasions for the different management treatments (C). Means (± SE) of 6 sites per management treatment are displayed. Different letters indicate significant differences according to post-hoc LSD-tests.

Were there broad associations between traits and management treatment responses? Results of the pooled analysis

The pooled analysis indicated that the least trait selection occurred at the grazed fields and at mulching twice per year (table 8).

At grazing, species with the ability for high lateral spread (>250 mm/year) were overrepresented in the group of the invaded species (adjusted residual= 2.7). Rosette species occurred more often in the group of the extinct species (adjusted residual= -2.0), while invaders tended to have regularly distributed leaves (adjusted residual= 2.0).

At mulching twice per year, like at grazing, species with high lateral spread were more often in the invader group than expected (adjusted residual= 2.8). Furthermore, species of the two groups differed in seed bank longevity. Invaders had significantly lower values of the seedbank longevity index (U= 1391.5, p= 0.034, n_{ex}= 75, n_{in}= 48).

At mulching once per year species were selected to have higher seed masses, while small seeded species got lost (U= 2677.5, p=0.023, n_{ex}= 104, n_{in}= 65). Like at mulching twice per year the seedbank longevity index of the invaded species was lower than that of the extinct species (U= 2396.0, p=0.001, n_{ex}= 106, n_{in}= 65). Furthermore, invaders had a higher canopy

height than extinct species (U= 1769.5, p= 0.014, n_{ex}= 108, n_{in}= 66) and lower Ellenberg values for light (U= 2693.5, p=0.007, n_{ex}= 106, n_{in}= 66).

Burning once per year led to a selection pressure towards species with spring germination (adjusted residual= 2.3), while all year germinating species were more often in the group of the extinct species (adjusted residual= -2.6). In the group of the invaded species canopy height was significantly higher (U= 2633.5, p= 0.049, n_{ex}= 104, n_{in}= 62) and Ellenberg indicator values for light (U= 2194.0, p= 0.001, n_{ex}= 100, n_{in}= 61), moisture (U= 1093.0, p= 0.000, n_{ex}= 83, n_{in}= 42) and nutrients (U= 1757.0, p= 0.045, n_{ex}= 83, n_{in}=53) were significantly lower.

The strongest trait selection occurred at abandonment. Like at burning, spring germination was enhanced (adjusted residual= 4.2), while all year germinating species went extinct more often (adjusted residual= -3.2). The selection for high competitive strength was most prevalent at this treatment. Poor competitors went extinct, while strong competitors invaded: high canopy height (U= 2126.5, p=0.002, n_{ex}= 145, n_{in}= 43), regularly distributed leaves (adjusted residual= 4.0), late seed shedding start (U= 2211.5, p= 0.009 , n_{ex}= 140, n_{in}= 42) and high Ellenberg values for nutrients (U= 1555.5, p= 0.024, n_{ex}= 108, n_{in}= 38) and low values for light (U= 2217.0, p= 0.015, n_{ex}= 137, n_{in}= 42) were promoted. Also species with high lateral spread (adjusted residual= 2.1) and therophytes (adjusted residual= 2.2) were more often in the group of the invaders, while non-therophyte species with small lateral spread (<100 mm/year) (adjusted residual= -2.8) were more often represented in the extinct species group.

The functional group affiliation based on a former study on functional group composition at different management treatments (chapter 2) confirmed the significant increase of competitive species belonging to the ”competitors”-group (adjusted residual= 3.8), while species of the “opportunists”-group (adjusted residual= -2.8), which were dominant at the grazing treatment in the former study, declined significantly at the abandonment treatment.

Table 8: Results of the pooled analysis. Mean trait values and relative attribute proportions of invaded (in) and extinct (ex) species for the different management treatments over all study sites (N= 6) and results of the Mann-Whitney U-tests and Chi²-tests. Only significant p-values are indicated: *= p<0.05, **= p<0.01, ***= p<0.001. Arrows indicate if trait values were higher (↑) or lower (↓) in the invader group (for p<0.05 and absolute values of adjusted residuals >2).

	invaded versus extinct species														
	grazing			**mulching twice**			**mulching once**			**burning once**			**abandonment**		
	mean			mean			mean			mean			mean		
	ex	in	U-test/ Chi²	ex	in	U-test/ Chi²	ex	in	U-test/ Chi²	ex	in	U-test/ Chi²	ex	in	U-test/ Chi²
seed mass	1.6	2.0		1.6	1.9		**1.3**	**3.2**	↑*	1.6	2.7		1.8	4.3	
seedbank longevity index	0.15	0.18		**0.18**	**0.12**	↓*	**0.18**	**0.12**	↓***	0.16	0.15		0.14	0.16	
emergence season:												*			***
spring	0.3	0.3		0.4	0.3		0.3	0.4		**0.3**	**0.5**	↑	**0.3**	**0.6**	↑
autumn	0.1	0.2		0.1	0.1		0.1	0.1		0.1	0.1		0.1	0.0	
all year	0.6	0.5		0.5	0.6		0.6	0.5		**0.6**	**0.4**	↓	**0.6**	**0.4**	↓
min. germination temperature	10.7	9.2		9.0	7.6		7.8	8.7		8.4	10.1		9.0	10.1	
light for germination:															
L=D	0.5	0.4		0.4	0.5		0.5	0.5		0.4	0.3		0.5	0.3	
L>D	0.5	0.6		0.6	0.4		0.5	0.5		0.6	0.7		0.5	0.7	
dormancy:															
no	0.4	0.3		0.4	0.5		0.4	0.3		0.4	0.3		0.4	0.3	
physiological	0.5	0.5		0.4	0.4		0.4	0.5		0.4	0.5		0.4	0.6	
physical	0.1	0.1		0.2	0.2		0.2	0.1		0.2	0.2		0.2	0.1	
canopy height	0.30	0.34		0.35	0.38		**0.32**	**0.42**	↑*	**0.32**	**0.43**	↑*	**0.32**	**0.55**	↑**
SLA	25.2	25.7		25.1	25.1		24.6	25.4		25.0	24.7		24.3	26.0	
vegetative lateral spread:			*			*									**
very small (therophytes)	0.1	0.2		0.1	0.0		0.1	0.2		0.1	0.1		**0.1**	**0.2**	↑
< 100 mm	0.3	0.3		0.5	0.4		0.3	0.4		0.4	0.4		**0.4**	**0.2**	↓
100-250 mm	0.4	0.3		0.3	0.3		0.4	0.3		0.3	0.3		0.3	0.3	
> 250 mm	**0.0**	**0.3**	↑	**0.1**	**0.3**	↑	0.2	0.2		0.2	0.2		**0.1**	**0.3**	↑
leaf distribution:			*												***
regularly	**0.1**	**0.3**	↑	0.1	0.2		0.2	0.3		0.2	0.3		**0.2**	**0.4**	↑
semi-rosette	0.8	0.7		0.8	0.6		0.8	0.6		0.7	0.6		**0.7**	**0.5**	↓
rosette	**0.1**	**0.0**	↓	0.1	0.1		0.1	0.1		0.1	0.1		0.1	0.1	
legume	0.1	0.1		0.2	0.2		0.2	0.1		0.1	0.1		0.2	0.1	
woodiness:															
non-woody	1.0	0.9		1.0	0.9		0.9	0.9		0.9	0.8		0.9	0.9	
semi-woody	0.0	0.1		0.0	0.1		0.1	0.1		0.0	0.1		0.0	0.1	
woody	0.0	0.1		0.0	0.1		0.1	0.1		0.1	0.1		0.0	0.0	
grass	0.2	0.2		0.2	0.2		0.2	0.2		0.2	0.2		0.2	0.2	
minimum bud bank depth:															
soil-surface	0.1	0.0		0.1	0.2		0.1	0.1		0.2	0.1		0.1	0.1	
0-10cm	0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0		0.0	0.0	
>10cm	0.9	0.9		0.9	0.7		0.9	0.9		0.8	0.9		0.8	0.8	
seed shedding earliest month	6.7	6.7		6.5	6.6		6.4	6.7		6.5	6.7		**6.4**	**7.0**	↑**
seed shedding latest month	10.8	10.5		10.3	10.6		10.3	10.4		10.4	10.2		10.5	10.5	
seed shedding duration	5.1	4.7		4.8	5.0		4.9	4.8		4.9	4.5		5.1	4.5	
Ellenberg N	4.2	4.1		4.2	4.2		4.0	4.5		**4.4**	**3.7**	↓*	**3.9**	**4.8**	↑*
Ellenberg F	4.4	4.3		4.7	4.6		4.5	4.4		**4.9**	**4.2**	↓***	4.6	4.4	
Ellenberg L	7.2	6.9		7.1	7.1		**7.2**	**6.8**	↓**	**7.2**	**6.8**	↓**	**7.2**	**6.7**	↓*
functional group:															**
"competitors"	0.2	0.4		0.4	0.3		0.3	0.4		0.3	0.4		**0.3**	**0.6**	↑
"rosettes"	0.1	0.1		0.1	0.2		0.1	0.1		0.1	0.2		0.1	0.1	
"legumes"	0.1	0.1		0.2	0.2		0.2	0.1		0.2	0.2		0.2	0.1	
"opportunists"	0.5	0.4		0.3	0.3		0.4	0.3		0.4	0.3		**0.4**	**0.2**	↓

Were there relationships between traits and trait selection within studies and were they consistent across study sites? Results of the meta-analysis

Next, we wanted to ensure that the broad patterns found in the pooled analysis were not a result of pooling. With the meta-analysis we tested for trait selections within study sites and for combined effects across study sites.

Trait effects reached at most medium mean weighted effect sizes (d= 0.5 to 0.8) when calculated as Hedges d (table 9). The patterns of effect sizes backed up the results of the pooled analysis to a large extent. Traits which reached at least a Hedges d value of 0.5 were mostly also significant in the pooled analysis and thus may be considered as most important for species selection at the different management regimes.

Therewith, only single findings of the pooled analysis may be qualified based on the meta-analysis. At grazing the selection for lower Ellenberg indicator values for light had the highest effect size of all traits (d= -0.58), while the selection against rosettes reached only a small effect size (d= -0.26). At burning once per year the promotion of the competitor group had an almost medium effect size (d= 0.48).

Furthermore, the meta-analysis revealed some general patterns of trait selection over all management treatments. At all management treatments species with higher canopy height (d= 0.21 to 0.76), regularly distributed leaves (d= 0.31 to 0.59) and lower Ellenberg values for light (d= -0.28 to -0.58) were promoted. Therewith, invaders and extinct species tended to differ in this set of traits at all management treatments. Only the dimension of the selection pressure differed as indicated by small to medium effect sizes dependent on the management treatment.

Mulching twice per year was separated from the other management treatments by several trait effects. It was the only management treatment at which spring germinating species (d= -0.24) and species with light demanding germination (d= -0.31) were overrepresented in the group of extinct species and at which the functional group of the “competitors” was not promoted (d= -0.13 at mulching twice, other treatments d= 0.31 to 0.63).

Table 9: Results of the meta-analysis. Mean weighted effect sizes (d) are given. Positive values of effect sizes (d) indicate higher trait values in the invader group. Effect sizes (d) are marked according to their magnitude: •= small effect (>0.2), ••= medium effect (>0.5), •••= large effect (>0.8).

	invaded versus extinct species				
	grazing	**mulching twice**	**mulching once**	**burning once**	**abandonment**
	d	d	d	d	d
seed mass	0.12	0.16	0.57 ••	0.17	0.31 •
seedbank longevity index	0.22 •	-0.51 ••	-0.51 ••	-0.07	0.10
emergence season:					
spring	0.25 •	-0.24 •	0.23 •	0.51 ••	0.74 ••
autumn	0.19	0.07	-0.11	0.02	-0.33 •
all year	-0.41 •	0.17	-0.16	-0.51 ••	-0.53 ••
minimum germination temperature	-0.25 •	-0.47 •	0.13	0.35 •	0.25 •
light for germination:					
L=D	-0.08	0.35 •	-0.10	-0.34 •	-0.33 •
L>D	0.08	-0.31 •	0.11	0.40 •	0.38 •
dormancy:					
no	-0.34 •	0.25 •	-0.17	-0.18	-0.15
physiological	0.19	-0.27 •	0.27 •	0.29 •	0.32 •
physical	0.19	0.06	-0.12	-0.17	-0.27 •
canopy height	0.21 •	0.30 •	0.49 •	0.61 ••	0.76 ••
SLA	0.15	0.09	0.13	-0.01	0.20 •
vegetative lateral spread:					
very small (therophytes)	0.07	-0.25 •	0.14	0.08	0.38 •
<100 mm	0.08	-0.18	-0.01	-0.07	-0.50 ••
100-250 mm	-0.44 •	-0.03	-0.16	-0.09	-0.03
>250 mm	0.58 ••	0.54 ••	0.13	0.14	0.40 •
leaf distribution:					
regularly	0.42 •	0.37 •	0.31 •	0.33 •	0.59 ••
semi-rosette	-0.18	-0.32 •	-0.29 •	-0.23 •	-0.50 ••
rosette	-0.26 •	0.02	0.05	-0.13	-0.11
legume	-0.10	0.08	-0.10	-0.11	-0.29 •
woodiness:					
non-woody	-0.20 •	-0.13	0.03	-0.32 •	-0.19
semi-woody	0.05	-0.10	0.05	0.39 •	0.31 •
woody	0.20 •	0.25 •	-0.05	0.02	-0.06
grass	0.15	-0.04	0.17	0.12	-0.06
minimum bud bank depth:					
soil-surface	-0.21 •	0.30 •	-0.08	-0.39 •	-0.06
0 - 10 cm	0.00	0.00	0.00	0.00	0.00
> 10 cm	0.11	-0.27 •	0.06	0.21 •	-0.04
seed shedding earliest month	0.04	0.26 •	0.19	0.34 •	0.40 •
seed shedding latest month	-0.29 •	0.17	0.06	-0.19	-0.04
seed shedding duration	-0.33 •	0.03	-0.12	-0.43 •	-0.29 •
Ellenberg N	0.02	0.08	0.30 •	-0.35 •	0.39 •
Ellenberg F	0.05	0.09	0.01	-0.45 •	-0.05
Ellenberg L	-0.58 ••	-0.28 •	-0.48 •	-0.54 ••	-0.41 •
functional group:					
"competitors"	0.31 •	-0.13	0.34 •	0.48 •	0.63 ••
"rosettes"	-0.17	0.07	-0.03	0.03	0.01
"legumes"	0.08	0.21 •	-0.19	-0.10	-0.24 •
"opportunists"	-0.22 •	-0.05	-0.17	-0.40 •	-0.46 •

Discussion

Invasion and extinction rates at different management treatments

The results confirmed that grazing is the management which best promotes species coexistence. Over all study sites the least extinctions occurred at grazing and mulching twice per year. Thus, most of the species present in 1975 persisted on the permanent plots until 2008. This result reflects the results of a former study on the development of plant functional group composition at differently managed fields (chapter 2). In this study grazing best succeeded to allow different functional groups to co-exist without negative influence on one another, while more extensive managements clearly promoted a highly competitive species group, which led to a decline of other functional group covers.

Grazing was the only management at which the mean number of invasions exceeded the number of extinctions and thus led to a species number increase at most sites. The promotion of species richness by large herbivore grazers in temperate grasslands has been recognized as general effect (Olff & Ritchie 1998). This originates from a multitude of mechanisms: large grazers create frequent, small disturbances and therewith regeneration sites and soil heterogeneity and serve as efficient seed dispersers (Olff & Ritchie 1998).

Other management treatments led to higher extinction numbers that were not compensated by invasions. Therewith, management treatments with higher extinction numbers tended to decrease in species numbers. That a decrease in intensity and/or frequency of disturbance regime can lead to decreasing species diversity has been noted (Wells 1969).

Invasion numbers relative to the initial species sets did not differ between the management treatments of the single sites. This could originate either from seed limitation, from very low establishment success at all management treatments or a combination of both factors. Seed limitation has been shown to be generally low in mesic grasslands (Turnbull *et al.* 2000). Nevertheless, even if germination is not hampered by biotic or abiotic factors, seedling mortality in grassland proofed to be very high and hardly any seedling may reach adult stage and reproduce (Miles 1972; Grubb 1977; Silvertown & Dickie 1980; Kiviniemi & Eriksson 1999, chapter 4).

Furthermore, germination niches will be mostly occupied by the seed rain of the neighbouring plants (Harper 1977; Verkaar *et al.* 1983a; Poschlod *et al.* 1996; Poschlod *et al.* 2005b).

Which trait selection pressures acted at the different management treatments?

Grazing

Though grazing was included as reference treatment, the results, especially of the meta-analysis, showed that trait selection pressures existed even at this treatment.

Nevertheless, besides mulching twice per year, grazing was the management treatment with least functional trait divergence between extinct and invading species. Thus, it promoted the coexistence of species with different strategies and traits. That grazing supports high species and functional trait diversity in grasslands is long known (Grubb 1986). Basically, those species rich grasslands evolved under grazing treatment which was often accompanied by manual prevention of shrub and tree encroachment. Traditional grazing facilitates the coexistence of species that depend on bare ground (Grubb 1976), low sward (Antonsen & Olsson 2005) and/or open structure (Pykälä *et al.* 2005) and of highly competitive species at the same time. Those competitive species get selectively suppressed at grazing treatments and competitive exclusion of the less competitive species is prevented (Grubb 1986; Klimes & Klimešová 2002; Grime 2006).

Nevertheless, our results indicated changes in functional trait composition of the grazed grassland sites. This may be mirroring the irregularities in the grazing treatments due to organizational problems. Grazing animals and stocking rates changed over the years, fertilizing events occurred and shrub encroachment and/or increased shading by trees were not prevented effectively at the different sites (Schreiber *et al.* 2009). Therewith, grazing failed to resemble "traditional grazing practice" completely. This is even more the case as the grazing animals lost their function as seed dispersers for typical grassland species as they do not get into contact with other species rich grasslands but the single study sites (Schreiber 2005). Due to increased shrub encroachment and nutrient inputs, species selection patterns indicated higher shading levels by selection for species with lower Ellenberg values for light and increased competition (dependent on site: caused by nutrient inputs or reduced grazing pressure) by selection for species with regularly distributed leaves.

Mulching twice per year

Overall, like at grazing, trait selection was low at mulching twice per year. Extinct and invading species were more or less randomly distributed across functional trait groups. Therewith, land-use change did not lead to a disproportional removal of species with certain

functional traits and losses of functional diversity should be a minor threat at mulching twice per year and grazing in comparison to the other management treatments.

Mulching twice per year was the only management at which species with spring germination and species belonging to the "competitors"-group got not enhanced, while non dormant species with light independent germination were more often in the invader group. Light dependent germination has been shown to be typical for competitive ruderals which may invade at the less intensive treatments, while light independent germination proofed to be typical for grassland species (Fenner 1978). Thus, even more than grazing treatment, mulching twice per year seemed to allow balanced competition at our study sites, as potential dominants got suppressed and competitive exclusion of typical grassland species was prevented. Contradictory, Kornas (1991) reported a loss of typical grassland species at mulching twice per year in hay meadows. Nowak and Schulz (2002) stated that mulching always fails to prevent eutrophication. Our results showed that at least no selection pressure existed towards species with higher nutrient demands regarding invading and extinct species.

Like at grazing, species with high lateral spread were promoted at mulching twice per year. Cutting twice per year often prevents successful flowering and seed production so that clonal species are enhanced (Poschlod *et al.* in press). Models on the impact of different disturbance levels on functional trait distribution also predicted promotion of species with high lateral spread at high disturbance levels (Kleyer 1999). That mulching twice represents a more intense disturbance level may also be reflected by selection for species with highest buds at soil surface, what may be an adaptation to frequent biomass removal close to the ground.

Mulching once per year

At mulching once per year invaders had higher canopy heights than extinct species, lower Ellenberg values for light and significantly higher seed masses.

According to Kleyer (1999) typical adaptations to reduced herbage use are taller stature and larger seeds. Therefore, selection pressures at mulching once per year represented on the one hand an extensification in comparison to grazing or mulching twice per year.

The strongest trait selection pressures at this treatment were those for higher seed masses and for lower seed bank longevity indices. Besides the explanation that more competitive species tend to have higher seed masses, the special environmental conditions at this mulching treatment may enforce the possession of large seeds for successful regenerative reproduction. At mulching once per year in August/September the organic matter decomposes quite slowly and therewith species have to cope with a dense litter layer at germination. In general, only

species with large seeds are able to establish in close vegetation or beneath litter (Grime 1979; Thompson 1987; Molofsky & Augspurger 1992; Schütz 2000). The influence of the accumulated litter on species composition has also been supposed by Moog (2002). According to our results, this effect of litter on species composition may be explained by selection for higher seed masses and by the promotion of vigorously growing plants as litter also increases soil moisture and nitrification (Schiefer 1982).

The selection for lower seed bank longevity may be a side effect of the selection for higher seed masses since seed size is generally linked to seed bank behavior (Thompson 1987; Bekker *et al.* 1998), so that species with larger seeds do not tend to form seed banks.

Burning once per year

Trait selection at burning was most similar to trait selection at abandonment. Species with high stature, low Ellenberg values for light and spring germination were more often in the invader group.

The selection for higher stature reached the highest effect size and also the selection for species belonging to the "competitor"-group reached almost a medium effect size. Therewith, adaptation to highly competitive environments should have been most important for species selection.

Spring germinating species were predicted to take advantage at burning (Schütz 2000; Poschlod *et al.* in press). Especially the ample availability of bare ground combined with little competition by the standing vegetation after winter burning should enlarge the chance of successful establishment of spring germinating species. Seedlings of all year or autumn germinating species may be harmed by burning to a large extent instead.

Unique to the burning treatment was the tendency for lower Ellenberg indicator values for nutrients and moisture in the invader group.

Fire affects plant available nutrients through the loss of nutrient elements in the smoke (nutrient outtake) and through the ash deposit (fertilizing effect). Though several authors compared burning to fertilization due to the sudden nutrient release by the ash deposit (Briemle 1991; Goldammer *et al.* 1997), it has been shown that burning removes comparatively high amounts of nitrogen and also other nutrients fixed in the above-ground biomass (Lloyd 1971; Niemeyer *et al.* 2005). Our results indicated that, though higher statured species got enhanced, this selection was not linked to an enhancement of higher nutrient demand. Therewith, no fertilization effect of burning seemed to affect species assembly processes at the burning treatments.

Also the selection for species with lower Ellenberg indicator values for moisture demonstrated that, besides the tendency to select for higher competitive species over all management treatments, selections typical for one management occurred. The selection for species with lower Ellenberg indicator values for moisture may be due to the fact that fire removes the litter layer which otherwise improves soil moisture conditions (Dierschke 1985). Elimination of moisture sensitive species at winter burning management has been reported (Fynn *et al.* 2004) and accordingly unfavorable soil moisture conditions were measured at burned sites in comparison to unburned control plots (Kelting 1957).

Abandonment

The selection pressure for competitiveness was most prevalent at the abandoned fields over all study sites. At abandonment the three highest effect sizes of the meta-study were reached. These indicated strong selection pressure for higher canopy height, for spring germination and for species belonging to the "competitor-"group.

More traits, also conferring higher competitiveness, were promoted, like regularly distributed leaves, high Ellenberg indicator values for nutrients, low indicator values for light and high lateral spread.

As seasonal timing determines the degree of competition for light, succession favors spring germinating species (Schütz 2000), while all year germinating species, which are adapted to germinate in gaps during the growing season, and to a lower extent autumn germinating species, are disadvantaged.

Nutrient enrichment at abandonment is typical, as no nutrients get removed, while airborne N-deposition (Pauli *et al.* 2002; Bobbink & Roelofs 2005; Smart *et al.* 2005) and increased nitrification through improved moisture conditions by dense litter layers (Dierschke 1985) additionally increase nutrient availability. While canopy height is generally positively correlated with competitive dominance (Gaudet & Keddy 1988; Hodgson *et al.* 1999; Weiher *et al.* 1999), it also positively correlates with nutrient availability in the case of succession (Diekmann & Falkengren-Grerup 2002).

Like at the more intensive management treatments grazing or mulching twice per year, high lateral spread (guerilla tactic) is also advantageous at succession (Prach & Pysek 1994) as clonal plants rely little on seedling recruitment (Eriksson 1997). Whereas seed production may be hampered at the more intense treatments, unfavourable germination conditions due to litter accumulation and high standing crop may prevent successful germination at succession (chapter 4).

Management independent trends of trait selection

The meta-study revealed common differences between invaders and extinct species over all management treatments and study sites. The selection pressure for higher canopy height increased from grazing, mulching twice, mulching once and burning to abandonment. On one of the study sites biomass measurements indicated an increase in fertility from grazing, mulching twice, mulching once to burning (Schreiber 2001). The increased biomass should intensify the competition for light (Campbell & Grime 1992). While the expected increases in canopy height along this gradient could not be validated using relative trait abundance values (Kahmen & Poschlod 2008b), the meta-study on invaders and extinct species visualized the increasing trend of this selection pressures from grazing to burning.

That higher canopy height should always be superior as long as grassland is not mown monthly has also been predicted by former models (Lehsten & Kleyer 2007). Pakeman and Marriott (2010) validated their hypothesis that plant trait responses to abandonment were similar to responses to extensification, differing only in the size of response. In Pakeman and Marriott´s study (2010) as well as in ours this was especially true regarding the traits canopy height and leaf distribution. Trait selection pressures at the alternative treatments to grazing in our study indicated that they all constitute different degrees of extensification.

The overall differences between extinct and invading species display a global pattern. Short statured species are considered to be especially vulnerable to extinction in open environments (Leach & Givnish 1996; Duncan & Young 2000; Blomqvist *et al.* 2003). Duncan and Young (2000) documented that tall, common species are much more successful than rare, short species over a range of habitats in New Zealand. Shifts in disturbance were held responsible for these trait based species selections.

The increasing selection for higher stature with decreasing management intensity may depict the shift from stress syndrome to competitive syndrome as predicted by Kleyer´s model (1999). Biomass and also canopy height have been shown to positively correlate with competitive ability of a plant (Gaudet & Keddy 1988).

Conclusions

It has been proposed that the best grassland management should be a disturbance to typical (or historic) levels to which native species are more likely to be adapted (Buckland *et al.* 2001). The current study supported this view, as the traditional grazing treatments, besides mulching twice per year, best succeeded to keep up functional diversity in terms of extinct and invaded

species traits. Low extinction numbers reinforced low trait selection pressures at the grazing treatment. Therewith, grazing offered best conditions for the coexistence of a variety of grassland species independent of their traits. Only mulching twice per year showed comparably low trait selection as grazing. Besides the overall promotion of higher competitive species, management specific selection patterns could be revealed, e.g. the strong selection for higher seed masses at mulching once per year or the selection for species with lower Ellenberg values for nutrients and moisture at burning once per year.

Chapter 4

Limitations to plant establishment in differently managed calcareous grassland

Abstract

To evaluate the relative roles of seed and germination niche limitation as well as seedling survival at different management treatments of calcareous grassland, we conducted a sowing experiment with 15 typical grassland species and followed species recruitment over three years. In half of the plots per grassland management treatment (grazing, burning once per year, mulching once per year and abandonment) litter and bryophyte cover were removed prior to sowing to simulate disturbance.

At most of the species germination rate was only significantly affected by the removal of litter and bryophyte cover and not by the management treatments. Seedling survival rate, however, was affected by the management treatment becoming the driving force for successful establishment.

The availability of germination niches plus the survival chances under different management regimes both influenced population development at differently managed grassland. The degree of seed limitation was low at all management treatments. Nevertheless, judging over abandonment, burning, mulching and grazing our results indicated, that the grazing treatment should offer best conditions for successful regeneration by seeds.

Introduction

Semi-natural calcareous grasslands originate from centuries of traditional management, i.e. grazing or mowing. In the last century those grasslands were considered increasingly as uneconomic and thus became threatened through abandonment, afforestration or intensification by fertilization. They belong to the most species-rich habitats in central Europe and harbor a great number of endangered and rare plant species (WallisDeVries *et al.* 2002).

One project that has been set up to find alternative, cost-effective management treatments to the traditional grazing management and to mowing, which was mostly applied as an alternative after the abandonment of grazing, are the “fallow experiments Baden

Württemberg". Within this project different management treatments (including grazing and mowing as control, mulching treatments, burning treatments and abandonment) were established to test their capability to maintain the species composition and richness of grasslands.

From the beginning of the fallow experiments until today species numbers declined at most of the management treatments (Poschlod *et al.* 2009b). Vegetation has still not reached a new stable state at the fields where alternative management treatments were applied. This concerns not only plant species (Poschlod *et al.* 2009b) but also plant functional group composition (Römermann *et al.* 2009, chapter 2). Thus, even 30 years after management change further extinctions of typical grassland species have to be expected.

By changing management regimes humans alter the environment and therewith the availability of dispersal, recruitment or reproductive niches of plants (Young *et al.* 2005, see box 1). Pollinators and seed dispersers can get lost.

While management changes affect survival of short-lived plants immediately, perennials can persist for decades without reproducing by seeds, when they are able to reproduce by vegetative means. This leads to the persistence of non-recruiting living deads (Janzen 2001) or relict populations (Eriksson 1996; Eriksson 2000). Tilman (1994) named this postponed extinction of populations "extinction debt".

Thus, only concentrating on actual species composition at the different management treatments may obscure the processes that lead to coming changes in species composition as the niches occupied by adults may be by far broader than the niches in which those species can set seeds and successfully recruit (Grubb 1977; Young *et al.* 2005).

As well for restoration and conservation practice as for the understanding of vegetation development and composition it is important to know about the extent of microsite limitation in contrast to seed limitation under different environmental conditions. Several studies addressed this question and came to mixed results dependent on studied ecosystem, environmental conditions and species (Eriksson & Ehrlén 1992 and citations therein). Seed limitation has been shown to decrease along gradients of productivity (Pärtel *et al.* 1996; Tilman 1997; Pärtel *et al.* 2000; Zobel *et al.* 2000; Foster 2001; Foster & Tilman 2003; Poschlod & Biewer 2005). Furthermore, forests are presumed to be more microsite limited than grasslands (Crawley 1990).

Here we conducted a sowing experiment on one site of the "fallow experiments" to investigate how different management regimes influence germination niche availability and seedling survival and thus the degree of seed limitation.

To trace back microsite limitation to germination niche limitation or limited survival chances we created artificial disturbances on half of the sown plots to reduce germination niche limitation at all tested management treatments.

Box 1: Definition of different types of ontogenetic niches (adapted from Young (2005)) and corresponding measures of niche limitation recorded in the sowing experiment.

Dispersal niche: The set of environmental parameters that determines where seeds arrive. This can be related to dispersal barriers as well as local dispersal limitations.

x: dispersal niche limitation was passed over by sowing (100 seeds per species and quadrat).
→ no recording.

Germination/Recruitment niche: The set of environmental parameters that allows seeds to germinate and become established (safe sites). This is similar to Grubb´s (1977) regeneration niche, which combines reproductive, dispersal and germination niches.

Germination: To estimate the number of germinated seeds, the number of seedlings per sown species was recorded in the first spring after sowing (in 2008).

Adult/Persistence niche: The set of environmental parameters that allows established plants to survive and grow. This is likely to be broader than other ontogenetic niches, both ecologically and biogeographically. Grubb (1977) calls this the "habitat niche".

Establishment: The number of seedlings per species was recorded in 2009 and 2010.
Survival rate: Percentage of germinated seeds that survived through the experiments running time.

Reproductive niche: The set of environmental parameters that allows adults to produce flowers, engage in successful fertilization, and rear seeds up to the dispersal stage. There is some evidence that the reproductive niche is narrower than the persistence niche.

Generative reproduction: Number of reproductive individuals per species and year (given in appendix 5) recorded in 2008, 2009 and 2010. Prerequisite for intergenerational persistence.

Working definition of the term seedling: for sake of convenience any small, non-reproductive plant is referred to as a seedling. Almost all individuals of the sown species fit into this definition. Only those that reached the reproductive stage during the study period definitely left the seedling stage and are referred to as flowering or reproductive individuals.

Material and Methods

Study site

In 1974 the project "Fallow experiments Baden-Württemberg" was initiated to study the suitability of different management regimes for maintaining the characteristic floristic composition of semi-natural grasslands. For our experiment we chose one calcareous grassland site belonging to the 14 study sites included in this project. This site, "St. Johann", is documented to have been continually used for sheep grazing since at least 1955. The vegetation is classified as Gentiano-Koelerietum (Schiefer 1981).

Like at all study sites of the fallow experiments an exclosure was set up at this site in 1974. This area was sub-divided into several strips, each strip being subjected to a specific management treatment since that time. The grazing treatment, as the original treatment, was

continued on a strip adjacent to the exclosure serving as reference treatment. For this study we focused on the four following treatments: extensive sheep grazing (twice per year), mulching once per year (late summer), burning once per year in winter and finally abandonment. Mulching resembles mowing but the biomass is chopped in small pieces and left at the site.

Seed addition experiment

Seeds of 15 forbs typical for the plant community of the study site and occurring in the regional but not in the local species pool of the study site at the start of the experiment were chosen for the seed addition experiment (appendix 3). The species were selected to represent a broad spectrum of plant strategies including short-lived and perennial species, species with regularly distributed leaves and semi-rosettes, species with and without persistent seed-bank etc..

Seeds for the experiment were purchased from commercial suppliers. For the majority of the species those seeds were derived from cultivations in the region of our study site.

At each of the four management treatments included in our study (grazing, burning once per year, mulching once per year and abandonment) 17 couples of two 90 cm x 90 cm plots lying next to each other were spread over the whole management treatment field (each approx. 30 – 60 m in length and 10 – 30 m in width). On half of the coupled plots moss and litter layer were removed by hand before sowing, on the other half no manipulation was applied.

For the sowing we applied three different kinds of species mixtures. Each sowing unit included 20 seeds of five different species (appendix 3). Each of the quadrats was subdivided in 10 cm x 10 cm subplots by a frequency frame. Five of these subplots were sown with one of the species mixtures to spread the risk of total germination failure of one species due to unforeseeable disturbances. Thus, 100 seeds per species and quadrat were sown in the first week of October 2007.

Preliminary germination tests under standardized light and temperature regimes and tetrazolium test served to determine the potential proportion of viable seeds for the seeds of each species. Information on germinability and viability of the seeds can be found in appendix 4.

Field assessments and data analysis

The study was conducted from October 2007 (sowing) to June 2010.

In spring 2008 germination was recorded to evaluate the role of germination niche limitation at the different management treatments (see box 1). In May 2008 we also recorded

environmental factors that may have been important for germination success for each of the 10 cm x 10 cm subplots: height and cover of vegetation, litter and moss layer and percentage cover of bare ground.

Subsequent establishment was recorded as number of seedlings alive in May 2009 and in June 2010. In addition to establishment we determined survival rates until 2010 based on germinated seeds. To calculate these survival rates we divided the number of individuals per species at the last observation date in 2010 by the maximum number of seedlings reached at previous observation dates (2008 or 2009). The number of established individuals and the survival rate were taken as measures for the availability of persistence niches.

The number of reproductive individuals per sown species was recorded each year. Individuals of most of the species, except *Anthyllis vulneraria* and *Rhinanthus minor*, have not yet flowered at the last recording date. Therewith, no final conclusion on the presence of reproductive niches at the different management treatments for most of the sown species could be made. Nevertheless, the calculated survival rate may also indicate a future trend for final reproductive success and thus intergenerational persistence.

To test for significant differences in environmental factors during germination at the different management regimes at quadrats with and without moss and litter removal, we applied non-parametric Kruskal-Wallis H-Tests followed by pairwise Mann-Whitney U-tests (with p-value adjustment method holm).

To analyse which environmental factors influenced germination success of the sown species at disturbed (moss/litter removal) and undisturbed quadrats we performed Spearman rank correlations to test for interrelations between germination success and environmental factors of the quadrats.

Next, we analyzed the effects of the different management regimes and artificial disturbances therein (moss/litter removal) on germination in 2008, on establishment in 2009 and in 2010 and on survival rates of the sown species.

To test if all species showed a general preference for the same management and reacted consistently to artificial disturbances through moss and litter removal, we performed non-parametric (rank) tests. First, mean numbers of individuals per species for the different years and for survival rates were tested with Wilcoxon signed rank test for differences between disturbed (moss/litter removal) and undisturbed quadrats per management treatment.

To test for a general ranking of management treatments regarding germination success, establishment success and survival rates of the sown species, we performed Friedman tests for related samples with means per species for disturbed and undisturbed quadrats.
We also analyzed germination success, establishment and survival for each species separately applying general linear models with management regime, disturbance (with/without moss and litter removal) and the interaction included as fixed factors. The zero inflation of our data set could best be handled by assigning a binomial error structure and a log link function to the models. These analyses were performed with library MASS (Venables & Ripley 2002) in R (R Development Core team 2004).

Phyteuma orbiculare was excluded from all analyses, since no germination could be recorded in the field or in the germination chamber.

Results

Development of germination, establishment and reproductive success from 2008 to 2010

In the first spring after sowing seedlings of all except one sown species were recorded. Almost all individuals of *Rhinanthus minor* even reached the reproductive stage at the first census in May 2008. *Phyteuma orbiculare* failed to germinate in the controlled germination experiment in the climate chamber as well as at all censuses of the sowing experiment though viability of the seeds was above 90 % (appendix 4, appendix 5).
In 2008 germination rates in the field of all species were by far lower than the viability and germination rates recorded in the climate chamber. In the field germination rates reached from 0 % (*Phyteuma orbiculare* at all treatments) to 18.9 % (*Centaurea scabiosa* at grazing treatment with disturbance, this value corresponded to 21.4 % germination based on viable seeds).
Germination of the hard coated, slow germinating *Ajuga genevensis* seeds has not been finished at the burning treatment at the first census 2008: seedling numbers in 2009 exceeded those in 2008. However, it was not possible to distinct between seedlings from the different years due to the slow growth rate of most species. The individuals of most of the species were still quite small and far from flowering at the end of the study.

Overall, seedling mortality at all management treatments was very high. No seedling of *Gentiana cruciata*, *Inula salicina*, *Saxifraga granulata* and *Teucrium botrys* survived until 2010 and also seedlings of most of the other species strongly declined in number over the

years and were very small at the last census. Therefore, it should be pointed out that due to small size of the majority of living plants in 2010 the results on long-term establishment chances are only preliminary for the majority of species, since further mortality has to be expected.

Only three of the sown species reached the reproductive stage during the study period: *Rhinanthus minor*, *Anthyllis vulneraria* and *Arabis hirsuta*.

Rhinanthus minor was the only strict annual species that germinated and produced seeds in the first and following years after sowing. *Rhinanthus minor* germinated at all management treatments at disturbed (moss and litter removal) as well as at undisturbed plots in 2008. Nevertheless, in 2010 no individual was counted at the burning treatment and also at abandonment the population sizes of *Rhinanthus minor* decreased over the years. In contrast, mean numbers of individuals increased at the quadrats with disturbance at mulching and at disturbed as well as at undisturbed quadrats at the grazing treatment. Therewith, *Rhinanthus minor* was the only species which proved to be neither germination niche nor reproductive niche limited at least at the grazing treatment and thus could be regarded as mainly seed-limited (before seed sowing) at this management treatment.

During the study period two individuals of *Anthyllis vulneraria* flowered at the burning treatment and two individuals flowered at the mulching treatment (appendix 5).

While flowering occurred only stochastically at the other treatments, in total 12 individuals of *Anthyllis vulneraria* flowered at grazing already in 2009 and the majority flowered at the disturbed plots and also half of the individuals at the undisturbed plots at the grazing treatment in 2010. Therewith, *Anthyllis vulneraria* had chances of long-term establishment at the grazing treatment, as this treatment offered germination niches as well as reproductive niches to this species.

One single individual of *Arabis hirsuta* at the grazing treatment and one at abandonment exceeded the other *Arabis hirsuta* seedlings by far in size and flowered in 2009. While new seedlings (at least +5) were recorded at the subplot at the grazing treatment in the following year, no seedling was recorded at the subplot at the abandonment treatment in the year after flowering.

Differences in environmental conditions at the management treatments in first spring after sowing

Germination relevant parameters differed significantly between the management treatments and between disturbed and undisturbed quadrats in the first spring after sowing (figure 5A-G).

The succession quadrats stood out by having the tallest vegetation in spring, while at all other treatments vegetation height was about 6 cm (figure 5A).

At the burning treatment moss and litter removal before the sowing procedure did not lead to significant differences in germination rates which was due to the fact that also the quadrats without removal had a high percentage cover of bare ground (figure 5G) and only little moss and litter cover in spring (figure 5C–F).

Also at the grazing treatment the removal of moss and litter before sowing did not change germination conditions of manipulated versus unmanipulated quadrats to a large extent (figure 5 A–G). Only bare ground availability increased significantly.

Most striking effects due to moss and litter removal were reached at the mulching once and at the abandonment treatment. The highest and thickest litter and moss covers were recorded at the undisturbed quadrats at the mulching and at the abandonment treatments in spring, while even at the unmanipulated quadrats moss and litter cover played a minor role at grazing and burning (figure 5C–F).

The cover of litter layer that accumulated until spring 2008 after removal in autumn at disturbed quadrats at mulching was comparable to the litter layer at burning and grazing (figure 5C). Only at abandonment new litter accumulated over winter at the disturbed quadrats.

The moss and litter removal led to a significant increase of bare ground to at least 25 % cover on average at mulching and abandonment (figure 5G). Therewith, differences between the disturbed quadrats of the different management treatments regarding bare ground availability were strongly reduced.

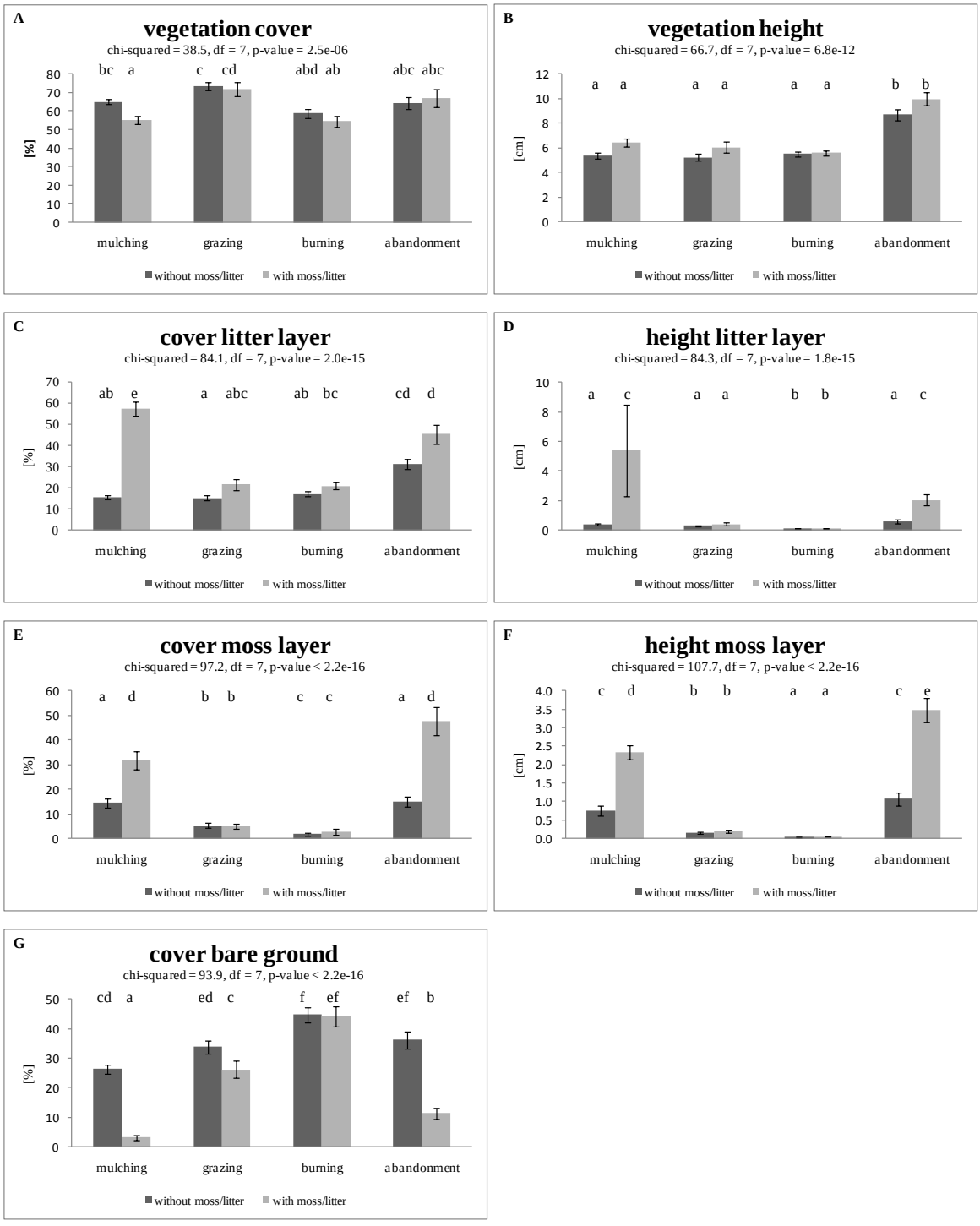

Figure 5: Means ± SE are given for germination relevant parameters recorded in spring 2008 at the different management treatments for quadrats with and without moss and litter layer removal at sowing. Kruskal-Wallis H-tests followed by pairwise Mann-Whitney U-tests (p-value adjustment method holm) were performed to detect differences between management treatments with and without moss and litter removal over all quadrats (n=17 per management and disturbance level (with and without moss and litter removal)). Different letters indicate significant differences according to pairwise Mann-Whitney U-tests.

Interrelation between germination conditions and germination success at quadrats with and without disturbance

The correlation between measured environmental parameters and the seedling numbers of the species showed that all species had more or less the same requirements for germination in the undisturbed quadrats (table 10A). Bare ground availability had a positive impact on seedling numbers for ten of the 15 sown species, while the cover and the height of the moss layer had a significant negative impact on these species. Likewise, the cover of the litter layer and its height had a significant negative impact on the majority of the species.

Overall, the correlations between environmental factors and seedling numbers at disturbed quadrats were much weaker, mostly not significant but much more species specific (table 10B). The availability of bare ground was no longer of primary importance for germination success and for *Centaurea scabiosa* seedling numbers were even negatively correlated with percentage cover of bare ground. Also cover and height of litter and moss layer, which partly redeveloped until the spring measurements after removal in 2007, were positively correlated with seedling numbers for some species at the disturbed quadrats.
The direction of the correlations with vegetation height and cover was also not consistent across species.

Table 10: Spearman correlations between seedling numbers and mean environmental parameters over all management treatments for disturbed (n=68) and undisturbed quadrats (n=68) recorded in spring 2008 (first spring after sowing). NA= not available (no seedlings). ***p<0.001, **p<0.01, *p<0.05.

A: Quadrats without disturbance

	vegetation height	vegetation cover	height litter	cover litter layer	cover moss layer	height moss	bare ground
Ajuga genevensis	-0.09	-0.14	-0.17	-0.20	-0.33 **	-0.37 **	0.25 *
Anthyllis vulneraria	-0.13	0.14	-0.31 **	-0.41 **	-0.33 **	-0.33 **	0.45 **
Arabis hirsuta	-0.55 **	-0.20	-0.67 **	-0.57 **	-0.73 **	-0.75 **	0.70 **
Buphthalmum salicifolium	-0.14	0.18	-0.47 **	-0.38 **	-0.49 **	-0.61 **	0.60 **
Centaurea scabiosa	-0.32 **	0.19	-0.21	-0.33 **	-0.41 **	-0.44 **	0.19
Crepis capillaris	-0.52 **	-0.16	-0.62 **	-0.59 **	-0.70 **	-0.75 **	0.66 **
Dianthus carthusianorum	-0.45 **	0.01	-0.60 **	-0.66 **	-0.64 **	-0.67 **	0.62 **
Galium glaucum	0.25 *	-0.09	0.27 *	0.22	0.21	0.14	-0.09
Gentiana cruciata	-0.15	0.21	-0.36 **	-0.26 *	-0.25 *	-0.37 **	0.29 *
Inula salicina	-0.07	-0.25 *	-0.38 **	-0.18	-0.31 *	-0.29 *	0.51 **
Origanum vulgare	-0.52 **	-0.19	-0.62 **	-0.49 **	-0.73 **	-0.77 **	0.67 **
Phyteuma orbiculare	NA	NA	NA	NA	NA	NA	NA
Rhinanthus minor	-0.12	0.24	-0.05	-0.24 *	-0.10	-0.15	0.13
Saxifraga granulata	-0.17	0.13	-0.14	-0.09	0.06	0.04	0.04
Teucrium botrys	-0.07	-0.06	-0.26 *	-0.24 *	-0.37 **	-0.29 *	0.28 *

B: Quadrats with disturbance (moss/litter removal in autumn 2007)

	vegetation height	vegetation cover	height litter	cover litter layer	cover moss layer	height moss	bare ground
Ajuga genevensis	-0.15	-0.04	-0.30 *	-0.21	-0.29 *	-0.31 *	0.46 **
Anthyllis vulneraria	-0.28 *	-0.04	0.23	-0.28 *	0.10	0.02	-0.09
Arabis hirsuta	0.02	-0.39 **	-0.15	0.30 *	-0.03	-0.06	0.43 **
Buphthalmum salicifoliu	-0.12	-0.23	0.15	0.07	0.11	-0.03	0.13
Centaurea scabiosa	-0.33 **	0.36 **	0.17	-0.47 **	0.04	-0.05	-0.28 *
Crepis capillaris	0.26 *	-0.16	0.27 *	0.23	0.15	0.16	0.09
Dianthus carthusianoru	0.31 **	0.05	0.28 *	0.24	0.07	0.10	0.22
Galium glaucum	0.03	0.16	-0.04	-0.14	0.10	0.04	0.19
Gentiana cruciata	-0.14	-0.12	0.13	0.21	0.27 *	0.13	0.06
Inula salicina	-0.33 **	0.04	-0.25 *	-0.37 **	-0.27 *	-0.31 **	0.20
Origanum vulgare	-0.02	-0.31 **	-0.01	0.22	0.09	0.06	0.30 *
Phyteuma orbiculare	NA	NA	NA	NA	NA	NA	NA
Rhinanthus minor	-0.19	0.13	-0.07	-0.31 *	-0.05	-0.11	-0.05
Saxifraga granulata	0.09	0.11	0.06	-0.09	0.15	0.19	0.09
Teucrium botrys	-0.13	0.18	-0.09	-0.04	-0.04	-0.18	0.01

Impact of disturbance (moss and litter removal) on seedling recruitment and survival at different management treatments

The analyses of the impact of moss and litter removal at the different management regimes on seedling recruitment showed a significant increase over all species at mulching and

abandonment but also at grazing and burning in 2008 (table 11), indicating gaps as limiting for the germination at all management regimes, at least to some extent.

That the effect of disturbance on seedling number was much stronger at mulching and abandonment than at the other treatments became apparent in the following two years, when seedling numbers had already declined (appendix 5). The significant differences in seedling numbers between disturbed and undisturbed quadrats were maintained only at abandonment and mulching (table 11).

At none of the four management treatments the moss and litter removal before sowing had a consistent effect on survival rates of the seedlings.

Table 11: Ranking of quadrats with moss and litter removal versus undisturbed quadrats for four management treatments according to Wilcoxon signed rank tests (N=14).

Analysed factor:		disturbance (moss and litter removal)			
Situation:	ranking*	abandonment p	grazing p	mulching p	burning p
germination 2008	yes > no	0.001 *	0.001 *	0.001 *	0.004 **
establishment 2009	yes > no	0.002 *	0.308	0.003 *	0.624
establishment 2010	yes > no	0.015 *	0.878	0.040 *	0.262
survival to 2010	yes = no	0.169	0.110	0.327	0.237

* the ranking was consistent when significant differences were found at one situation, hence ranking is not given for every management regime separately.

Impact of different management treatments on germination niche availability and on seedling survival at quadrats with and without disturbance (moss/litter removal)

with disturbance (moss/litter removal)

In 2008 at the disturbed quadrats no management offered better germination conditions than another treatment for the sown species (table 12). The seedling numbers (appendix 5) showed that some species had highest germination at succession (e.g. *Dianthus carthusianorum*) others at grazing (e.g. *Rhinanthus minor*) or burning (e.g. *Inula salicina*), dependent on species specific requirements for germination (table 10B), which apparently emerge when bare ground is no longer limiting.

Seedling numbers in the following year (2009) also did not show consistent preference for a specific management treatment (table 12). Only in the final year of recording (2010) differences between the management treatments became significant regarding the numbers of established individuals and survival rates. Finally, independent which management offered best germination conditions for the species in 2008, seedling mortality differed significantly

between the management treatments and led to consistent differences between the management treatments. Highest numbers of survived seedlings were found at the grazing treatment, while least seedlings were recorded at the burned field. Accordingly, survival rates were highest at grazing followed by abandonment and mulching and finally burning.

without disturbance

Without disturbance (moss and litter removal), management dependent differences in seedling numbers were significant already in the first spring after sowing. Grazing followed by burning offered best germination conditions, while least seedlings were recorded at succession and mulching. While management dependent differences were only marginally significant in 2009, the pattern was consolidated in 2010. Grazing was ranked on first place followed by burning, while abandonment and mulching were on the same rank.

Though only marginally significant, survival of the seedlings to 2010 was highest at grazing and lowest at burning, like at the disturbed quadrats.

Table 12: Ranking of quadrats of four management treatments for disturbed and undisturbed quadrats in Friedman tests for related samples (N=14). US= abandonment, 1M= mulching once per year (late summer), KBj= controlled burning once per year (winter), BW= sheep grazing (twice per year).

Analysed factor:	management treatment			
Situation:	ranking	with disturbance (moss and litter removal) p	ranking	without disturbance p
germination 2008	1M>US>BW>KBj	0.212	BW>KBj>1M>US	0.000 ***
establishment 2009	US>1M>BW>KBj	0.207	BW>KBj>1M>US	0.051 .
establishment 2010	BW>1M>US>KBj	0.012 *	BW>KBj>US=1M	0.027 *
survival rate 2010	BW>US>1M>KBj	0.015 *	BW>1M>US>KBj	0.098 .

Response to disturbance and management treatment on species level

The glm-analyses on species level confirmed the results of the previous analyses. Germination of all species, except *Teucrium botrys*, was significantly (only marginally significant for two species) promoted by the removal of the moss and litter layer before sowing (table 13A). Management treatment only influenced seedling numbers of three species in 2008.

Seedling numbers declined markedly for almost all species in the following years (appendix 5). Nevertheless, the effects of disturbance (moss and litter removal) on seedling numbers were transferred to 2009 for six species (including one marginally significant disturbance impact) and to 2010 for four species (table 13 B,C).

In 2010 seedlings of 10 of the 15 sown species had established. For four of the established species management dependent differences emerged in 2010. Also the first significant interaction between management treatment and disturbance was detected in 2010 (for *Rhinanthus minor*).

Analyzing survival rates to 2010 (table 13D) the interaction between management treatment and disturbance was significant for nine out of the ten species with survived seedlings in 2010.

Disturbance alone was a significant factor for survival rates of seven species. This means that higher seedling numbers due to disturbance raised the chance that at least one seedling survived. Nevertheless, the significant interaction term showed that the survival chances were highly management dependent and not only based on the initial number of seedlings in 2008.

Table 13: Results of the glm-analyses on species level (p values). Results for numbers of germinated seedlings in 2008 (A), for establishment until 2009 (B) and until 2010 (C) and for survival rates based on maximal seedling numbers counted in the single quadrats in previous years (D). -= no seedlings/no living individuals.

	A	**germination 2008**		**B**	**establishment to 2009**	
	management	disturbance	management x disturbance	management	disturbance	management x disturbance
Ajuga genevensis	0.573	0.003 **	0.614	0.315	0.187	0.075 .
Anthyllis vulneraria	0.889	0.000 ***	0.078 .	0.712	0.077 .	0.137
Arabis hirsuta	0.551	0.000 ***	0.302	0.057 .	0.001 ***	0.992
Buphthalmum salicifolium	0.511	0.000 ***	0.638	0.458	0.000 ***	0.998
Centaurea scabiosa	0.491	0.051 .	0.118	0.453	0.222	0.181
Crepis capillaris	0.456	0.000 ***	0.243	0.198	0.975	0.430
Dianthus carthusianorum	0.000 ***	0.000 ***	0.127	0.013 *	0.000 ***	0.207
Galium glaucum	0.888	0.000 ***	0.251	0.769	0.041 *	0.244
Gentiana cruciata	0.601	0.000 ***	0.684	0.433	0.560	0.142
Inula salicina	0.016 *	0.000 ***	0.839	0.522	0.265	0.408
Origanum vulgare	0.569	0.000 ***	0.882	0.283	0.000 ***	0.356
Phyteuma orbiculare	-	-	-	-	-	-
Rhinanthus minor	0.012 *	0.097 .	0.873	0.148	0.497	0.287
Saxifraga granulata	0.464	0.000 ***	0.247	0.096 .	0.239	1.000
Teucrium botrys	0.231	0.705	1.000	0.547	0.654	0.616

	C	**establishment to 2010**		**D**	**survival rate to 2010**	
	management	disturbance	management x disturbance	management	disturbance	management x disturbance
Ajuga genevensis	0.365	1.000	0.326	0.000 ***	0.000 ***	0.000 ***
Anthyllis vulneraria	0.567	0.586	0.380	0.000 ***	0.000 ***	0.000 ***
Arabis hirsuta	0.002 **	0.035 *	0.673	0.171	1.000	0.000 ***
Buphthalmum salicifolium	0.371	0.735	0.244	0.000 ***	0.000 ***	0.000 ***
Centaurea scabiosa	0.643	0.431	0.158	0.000 ***	0.000 **	0.002 **
Crepis capillaris	0.893	0.049 *	0.652	0.810 ***	0.817	0.691 ***
Dianthus carthusianorum	0.363	0.422	0.963	0.006 ***	0.024 ***	0.000 ***
Galium glaucum	0.000 ***	0.673	0.194	0.000 ***	0.000 ***	0.000 ***
Gentiana cruciata	-	-	-	-	-	-
Inula salicina	-	-	-	-	-	-
Origanum vulgare	0.035 *	0.005 **	0.987	0.280	0.682	0.996
Phyteuma orbiculare	-	-	-	-	-	-
Rhinanthus minor	0.000 ***	0.002 **	0.000 ***	0.000 ***	0.000 ***	0.000 ***
Saxifraga granulata	-	-	-	-	-	-
Teucrium botrys	-	-	-	-	-	-

Discussion

Degree of seed limitation in mesic grasslands

For all species but *Phyteuma orbiculare,* which failed completely, germination rates in the field were much lower than the recorded germination rates in the climate chamber. This has also been found in other sowing experiments (Hutchings & Booth 1996a; Jackel 1998) and may be due to a combination of several factors: seed predation, pathogens, gaps, soil chemistry or unfavorable light, temperature and/or water conditions.

The unfavorable conditions for germination in grasslands are reflected by records of generally low seedling numbers in this ecosystem (Cavers & Harper 1967; Turkington *et al.* 1979; Barrett & Silander 1992). Nevertheless, management dependent differences in germination niche availability were obvious and will be discussed in the following sections.

Four of the species which germinated in the field went extinct at all tested management treatments until the end of the experiment. All species except *Rhinanthus minor* suffered high seedling mortality until 2010. Also the majority of established plants of almost all species was still very small and, except *Rhinanthus minor* and *Anthyllis vulneraria,* have not yet flowered in 2010. Very high seedling mortality in closed grassland swards is common (Miles 1972; Grubb 1977; Silvertown & Dickie 1980; Kiviniemi & Eriksson 1999). That seedlings stay very small over years in the presence of adult neighbour plants and finally often die without ever producing seeds, has also been reported by several authors (Miles 1972; Harper 1977; Silvertown & Dickie 1980; Stampfli & Zeiter 1999) and indicates that seedlings live under severe stress in closed grassland swards (Harper 1977). Most important stress factors are the interference with adult neighbour plants (Peart 1989), physical hazards like frost or drought and pathogens (Ryser 1993; Hutchings & Booth 1996a).

A meta-study on seed limitation in different ecosystems (Turnbull *et al.* 2000) confirmed the overall low degree of seed limitation in mesic grassland: only in 20 % of the reviewed studies seed limitation could be demonstrated, while microsite limitation was clearly prevailing. The meta-study also found the heavy decline in sown species presence between seedling and adult stage stressing the importance of the study period for predictions on seed limitation versus microsite limitation. Eriksson (1996) calculated for his study on *Vaccinium myrtillus* that even under optimal environmental conditions no more than 0.3 % of the seeds will reach adult stage and reproduce.

Germination niche limitation at different management treatments of calcareous grassland

without disturbance

The overall higher germination at grazing followed by burning in comparison to the mulching or abandonment treatment could be easily explained by the environmental conditions at the different treatments. Seedling numbers depended on the availability of bare ground and were negatively correlated with cover and height of moss and litter layer, while vegetation height and cover were of secondary importance. The germination suppression by moss cover (Keizer *et al.* 1985; Spackova *et al.* 1998; Overbeck *et al.* 2003) and litter layer (Goldberg & Werner 1983b; Bosy & Reader 1995; Eriksson 1995; Hurst & John 1999; Xiong & Nilsson 1999; Schütz 2000) was demonstrated in several studies.

At the burning treatment the sown species may not only have been promoted by the bare ground availability, but also by heat shock or smoke derived compounds (Brown & van Staden 1997; Keeley & Fotheringham 2000; Bylebyl 2007) or by altered soil properties after fire. That overall seedling numbers at burning were ranked below grazing despite higher bare ground availability, could be due to damage of seeds and autumn germinated seedlings through fire.

with disturbance (moss/litter removal)

At the quadrats, where moss and litter layer were removed to simulate disturbance before sowing, seedling numbers were enhanced at all management treatments. That this disturbance also increased seedling numbers at burning, where moss and litter removal did not lead to any significant difference in the measured environmental factors in spring, may be explained by an improvement of soil texture through the disturbance. Harper (1965) had shown that differences in soil texture can improve germination conditions significantly.

Bare ground was no longer limiting at disturbed quadrats and no management offered best germination conditions for all species, supporting that bare ground, moss and litter layer were responsible for seedling numbers at undisturbed quadrats. Instead, species dependent differences emerged. Since bare ground of on average at least 25 % cover was offered at all management treatments, higher bare ground cover became even negatively correlated with seedling numbers of *Centaurea scabiosa*. Since seedling numbers of this species were also positively correlated with vegetation cover, it could be supposed that this large seeded species suffered more predation when seeds were more exposed. It has been shown that large seeded

species are much more prone to predation while vegetation cover does not hamper their germination (Reader 1993).

Survival and establishment chances of seedlings at different management treatments in relation to germination niche availability

The results of the non-parametric analyses as well as the results of the glms for the single species demonstrated that disturbance led to higher seedling numbers at all management treatments. However, the number of established individuals in 2010 was dependent on the management and not necessarily dependent on the initial seedling number.

Burning offered good conditions for germination of many species, what is in accordance with other studies reporting seedling flushes after burning (e.g. Peart 1984; Kitajima & Tilman 1996). Nevertheless, on the long run survival was lowest at the burning treatment and thus heavy mortality had occurred. One factor may be the heat damage as the fire usually burns heavier than intended and thus also destroys the litter layer, which should stay intact under optimal conditions. How far other factors, like predation, desiccation etc., are more important for seedling survival than at the other treatments could not be determined in this study.

Low establishment at abandonment and mulching could be better traced back to germination niche limitation, while survival was at least higher than at the burning treatment. Nevertheless, the number of flowering individuals at abandonment indicated that flowering was an absolute exception (one *Arabis hirsuta* plant in 2009) and did not lead to new seedlings in the following year. Strongly reduced regeneration after abandonment of meadows has also been found in other studies (Kahmen & Poschlod 2008a). Also at the mulching treatment only one *Anthyllis vulneraria* individual flowered at disturbed and undisturbed quadrats respectively until 2010.

Grazing offered germination niches and had the highest chances of seedling survival and therewith establishment. The outstanding conditions offered at the grazing treatment were also represented by successful generative reproduction of some species. *Rhinanthus minor* flowered and set seeds each year and achieved a significant population growth. Also many of the *Anthyllis vulneraria* plants flowered and set seeds at the grazing treatment in 2010. Furthermore, one individual of *Arabis hirsuta* set seeds in 2009 and new seedlings emerged the following year at the grazing treatment. The higher survival chances and good growth conditions at grazing may be due to reduced adult-seedling competition before peak standing crop is reached, while competition at the other treatments is not reduced at all during the growing season (at burning, abandonment) or only in the end of summer (at mulching). That

extensive grazing favors seedling recruitment has also been found by Oesterheld and Sala (1990).

Based on our results, especially considering the quadrats with moss and litter removal and the burning treatment, seedling survivorship seemed to override seedling emergence patterns comparing the different management regimes and thus final establishment is not going to reflect initial seedling numbers. Other studies on the importance of variation in germination for differences in establishment came to contrary results. Several authors found that the variation in germination and therewith germination niches determine differences in plant distribution and abundance (Miles 1972; Grubb 1977; Harper 1977; Reader 1991). Others found that conditions that favor germination do not necessarily favor seedling survivorship (Cavers & Harper 1967; Reader 1991; Schupp 1995; Eriksson & Fröborg 1996).

Conclusion

The experiment showed that seed limitation is low for typical grassland species under the four studied management treatments at our study site. Although germination was strongly dependent on gap availability at the different management treatments, further survival was negligible for most of the species at all management treatments. Nonetheless, survival chances differed between the management treatments.

Artificial gaps led to higher seedling numbers at all management treatments indicating some degree of germination niche limitation at all treatments. However, finally the management treatment influenced seedling survival and became the driving force for successful establishment. Judging over abandonment, burning, mulching and grazing our results indicated, that the grazing treatment offered best conditions for successful regeneration by seeds, for subsequent survival of seedlings and even for their generative reproduction.

Making predictions on the vegetation development at the different management treatments of the fallow experiments, our results imply that species numbers may further decline at the alternative management treatments due to reduced regeneration by seeds even when adult plants persisted since grazing ceased and even if seedlings may be abundant.

Chapter 5

Neighbourhood impact on plant invasion success in a calcareous pasture

Abstract

During the assembly process of a plant community several consecutive filters act on a potential new member. These filters operate on increasingly smaller scales starting with the dispersal filter so that only plants able to reach the specific site may be filtered out by the following filters imposed by climatic and edaphic conditions, disturbance regime and finally by biotic interactions.

The current study focused on this final filter and searched for mechanisms of biotic filtering in the invasion process of 15 plant species in a calcareous pasture. A sowing experiment with 15 plant species fitting in the plant community but not present on the site until the start of our experiment was conducted. The species were presumed to potentially pass the climatic, the edaphic and the disturbance filter, while the dispersal filter was passed over by sowing. Therefore, the focus could be put to biotic filtering processes imposed by neighbouring plant species. Germination of all species was artificially enhanced by moss and litter removal before sowing to get enough seedlings to be able to detect patterns of neighbourhood filtering influencing seedling survival and final establishment after three growing seasons. Several neighbourhood characteristics were recorded, like neighbour species identity and neighbour species traits in 10 cm radius around the seedlings, vegetation cover and height in spring and summer, bare ground, litter layer etc..

Next, plots with successful survival of the sown species until the last census were contrasted against plots that did not permit survival.

Establishment of all species was generally very poor and only individuals of eight species survived until the final census. Though many seedlings and juveniles may have died due to unforeseeable events, some patterns of possible neighbourhood filtering mechanisms emerged.

We found hints for facilitation playing a role, e.g. host species occurrence could have influenced *Rhinanthus minor* establishment. *Anthyllis vulneraria* tended to be more successful in plots with less cover of other legumes.

Species diversity turned out to be most significant in our analysis. The survival of all species tended to be higher in plots with higher species richness. On the one hand this could also point to the importance of facilitative effects as higher species richness might raise the chance of a species being present which facilitates invasion. On the other hand higher species richness was correlated with a number of other plot characteristics, like lower mean SLA values, lower mean Ellenberg N values and lower mean competitiveness values sensu Grime´s CSR strategy scheme etc.. These correlations mainly pointed to a less competitive environment at higher diversity plots.
Therewith, our study pointed out that also in natural systems mechanisms of biotic filtering through neighbouring plants may control small scale species assembly.

Introduction

At the beginning of the last century Clements (1928) noted that "the ecesis of the social plant is the same as that of an isolated invader in essentials, but it takes place under conditions modified by the neighbouring plants". That these modifications by neighbouring plants can have enormous impact on establishment success becomes evident by comparing species establishment in grassland communities on bare soil plots versus establishment in the closed sward (e.g. Turkington *et al.* 1979; Aguilera & Lauenroth 1995). While establishment on bare soil will be successful even over a broad range of abiotic conditions for many plants (constituting their fundamental niche sensu Hutchinson (1958)), with neighbouring plants the establishment will be hampered to a large extent even under conditions best meeting the species´ requirements (realized niche sensu Hutchinson 1958). Yet, the modifications by neighbouring plants and their influence on small scale invasibility are still not understood in entirety and under ongoing debate in basic ecology.
The difficulty in studying neighbourhood effects on invasibility consists in the complexity of the assembly processes of plant communities. Especially the assembly of species rich plant communities involves a complex chain of events (Grime 1979). Neighbouring plants affect each other by the consumption of resources, production of toxins and litter, by changing climatic conditions, since they protect from wind or change the small scale temperature regime, and by influencing the behaviour of predators, herbivores, pathogens etc. (Harper 1977). Additionally, the point in time when species enter the community is crucial for the species´ impact on each other and thus for the future community structure, as the outcome of seedling-seedling competition does not necessarily coincide with the outcome of seedling-adult or of adult-adult competition for two species (Crawley *et al.* 1999).

In order to understand how plant communities assemble, laborious reductionist analyses of single aspects of community assembly were undertaken. By this approach it could be shown that resource competition (Connell 1983; Hautier *et al.* 2009), allelopathy (Rice 1984) facilitation (Callaway 1995) and belowground competition (Casper & Jackson 1997) may have important effects on community organization.

Other studies chose the manipulation of single factors in natural systems to evaluate their impact on community structure, like predator exclusion (Reader 1993; Clear Hill & Silvertown 1997) or moss and litter removal experiments (Goldberg & Werner 1983a; Spackova *et al.* 1998; Stampfli & Zeiter 1999; Xiong & Nilsson 1999; Jensen & Gutekunst 2003; Overbeck *et al.* 2003; Maret & Wilson 2005).

Furthermore, studies using constructed communities dealt with the impact of species diversity, functional group diversity or species identity on invasibility (Turkington *et al.* 1979; Crawley *et al.* 1999; Naeem *et al.* 2000; Prieur-Richard *et al.* 2000; Fargione *et al.* 2003; Lanta & Leps 2006). Especially divergent results on the relationship between plant diversity and invasibility led to an ongoing debate questioning the importance of basic ecological hypotheses (see box 2).

One problem of studies on simplified and constructed communities is, that their results on single factor effects do not necessarily resemble the effect the same factor has in natural systems - just due to covarying extrinsic factors or higher order interactions (Clear Hill & Silvertown 1997; Hector *et al.* 2001) that have been removed when studying single factor effects in isolation.

Being aware of the complexity and entanglement of those neighbourhood interactions Harper (1977) advised not to study simple effects, confirming the statement of DeWit (1960 in Harper 1977), who stated that trying to subdivide the complex of plant interactions into particular components is "…not necessary, always inaccurate and therefore inadvisable". Harper (1977) merged the changes in environmental conditions brought about by the proximity of individuals in the term "interference" and therewith deliberately avoided to name the responsible mechanisms for neighbourhood effects on plant growth. A more recently coined term for patterns due to interactions between species are "assembly rules" sensu Wilson and Gitay (1995a), who wanted to clearly separate those species mediated patterns from environmentally mediated patterns. Nevertheless, biotic and abiotic effects are not acting isolated from each other in nature, such that, for example, disturbances brought about by grazers have direct influence on the strength of biotic effects and on the availability of

resources (Tilman & Pacala 1993). Thus, abiotic and biotic effects are almost impossible to disentangle in natural plant communities.

In the current study we decided to analyse neighbourhood effects on invasion success in a non-artificial system. Therefore we chose a sheep grazed calcareous grassland in SW-Germany as study site. These grasslands are among the world´s most diverse communities at the scale of one to several square meters (Kull & Zobel 1991). We chose a pasture as seedling recruitment plays a strong role for community structure in this habitat. It has been shown for this study site that grazing offers best conditions for regeneration by seeds, while other management regimes like mulching, burning or abandonment lead to negligible seedling recruitment (Poschlod *et al.* in press, chapter 4). Also other studies showed that seedling recruitment in pastures is important and that this also explains the high species richness of grazed grasslands (Watt & Gibson 1988; Oesterheld & Sala 1990). Therewith, the study of mechanisms underlying neighbourhood dependent invasion success could help to understand the small scale species composition in this habitat.

We performed a sowing experiment and recorded surrounding vegetation and gathered a multitude of variables to describe the invaders neighbourhood. The sedentary nature of plants makes the direct neighbourhood the scale to look for interactions among plants (Harper 1977). Therefore, we focused on a 10 cm radius around the sown plots (10 x 10 cm).

We wanted to see what remains of the neighbourhood´s effect on invasion success in a non-artificial ecosystem. Therefore, it had to be accepted that it would not be possible to attribute outcomes of invasion success to a single factor for sure. Rather, we looked for patterns giving evidences that processes like competition, allelopathy, facilitation, mutualism and other biotic interactions known in theory may actually affect real communities.

Box 2: Plant diversity and community invasibility

In community ecology the relationship between plant diversity and invasibility is still invoking controversies: negative, neutral as well as positive relationships have been postulated (reviews given by Levine & D'Antonio 1999; Hector *et al.* 2001; Wardle 2001; Fridley *et al.* 2007). The term "invasibility" emerged in the field of invasion ecology and refers to the susceptibility of an environment to the colonization and establishment of individuals from species not currently part of the resident community (Davis *et al.* 2005).
An important point of the "invasion paradox" is the scale dependence of the results (Fridley *et al.* 2007). In general, fine scale studies on the relationship between the number of native species and the number of invading exotics found a negative relationship, while large scale studies yielded the opposite result (Stohlgren *et al.* 1999; Brown & Peet 2003; Knight & Reich 2005).
Focusing on the small scale studies, the effects of diversity on invasibility are under ongoing debate. While one group claims that high diversity per se has negative effects on invasibility, as it could be demonstrated in experimental studies (e.g. Tilman 1997; Levine 2000; Naeem *et al.* 2000; Symstad 2000; Kennedy *et al.* 2002; Ruijven *et al.* 2003; Roscher *et al.* 2009a), others claim that diversity has neutral (e.g. Smith *et al.* 2004; Von Holle & Simberloff 2005; Emery & Gross 2006) or even positive effects on community invasibility (e.g. Palmer & Maurer 1997; Foster *et al.* 2002; Ejrnaes *et al.* 2006; Eriksson *et al.* 2006). This applies mostly to observational studies.

Assumed mechanisms for the **negative invasibility-diversity relationship** are:

- According to the diversity–invasibility hypothesis (Elton 1958) diversity leads to more complete utilization of limiting resources (this has been shown for the resources light, nutrients and space (Knops *et al.* 1999; Stachowicz *et al.* 1999; Naeem *et al.* 2000)) what in turn reduces invasibility. Mechanisms:
    - diversity–productivity relationship: greater chance that a more productive species would be present at higher diversity (the sampling effect) (Tilman 1999).
    - better ''coverage'' of habitat heterogeneity caused by the broader range of species traits in a more diverse community (the niche differentiation effect) (Tilman 1999).

Assumed mechanisms for the **neutral invasibility-diversity relationship** are:

- the dominant species identity determines invasibility (either positive or negative) (Smith *et al.* 2004; Emery & Gross 2006).
- propagule pressure overrides any possible effect of diversity (Von Holle & Simberloff 2005).

Assumed mechanisms for the **positive invasibility-diversity relationship** are:

- diversity begets diversity hypothesis: each plant species affects the environment differently, thus causing small-scale environmental heterogeneity again creating opportunities for species establishment with different requirements (mechanism: facilitation). (Palmer & Maurer 1997)
- diversity itself has no direct impact on invasibility:
    - diversity does not give rise to invasibility, but rather emerges from it (Davis *et al.* 2005; Eriksson *et al.* 2006)
    - diversity co-varies with extrinsic factors that control species richness and invasibility in natural systems, these factors contribute to spatial variation (disturbances, nutrient and/or light availability etc.) (Foster *et al.* 2002; Ruijven *et al.* 2003)

Methods

Study site

The study was conducted on a species rich calcareous grassland site of high conservation value in SW-Germany (760 m a.s.l., 6 - 6.5 °C mean temperature, 1000 mm precipitation/year). The site is documented to have been continually used for sheep grazing since at least 1955. The vegetation is classified as Gentiano-Koelerietum (Schiefer 1981).

Seed addition experiment

Seeds of 15 forbs typical for the plant community of the study site and occurring in the regional species pool but not present at the study site at the start of the experiment were chosen for the seed addition experiment (appendix 3). The species represent a broad spectrum of plant strategies including short-lived and perennial species, species with regularly distributed leaves and semi-rosettes, species with and without persistent seed-bank etc.. Seeds for the experiment were purchased from commercial suppliers. For the majority of the species those seeds were derived from cultivars of wild populations in the region of our study site.

17 90 cm x 90 cm quadrats were spread over the whole management treatment field. To reduce germination niche limitation and to provide sufficient seedling numbers to test for neighbourhood effects on seedling survival, moss and litter layer were removed by hand immediately before sowing.

For sowing, three different kinds of species mixtures were prepared. Each sowing unit included 20 seeds of five different species. Each of the quadrats was subdivided in 10 cm x 10 cm subplots by a frequency frame (figure 6). Five of these subplots were sown with one of the species mixtures in a latin square design. Thus 100 seeds per species and quadrat were sown in the first week of October 2007.

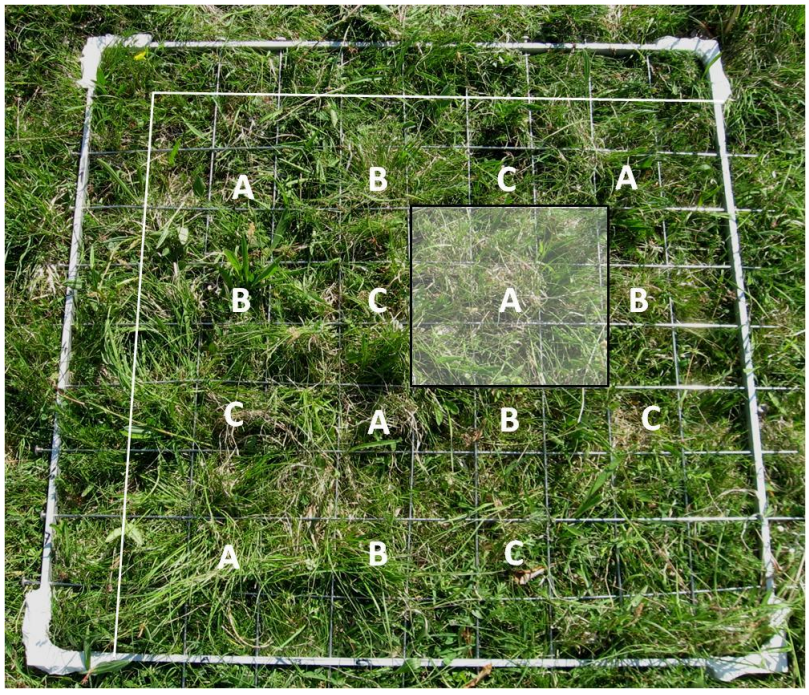

Figure 6: 90 x 90 cm quadrat with 15 10 x 10 cm subplots sown with one of three seed-mixtures (A, B, C) each. The shaded quadrat indicates the radius of one of the vegetation relevés for one of the subplots.

Field assessments and data analysis

Germination and establishment

The study was conducted from October 2007 (sowing) to June 2010 (final establishment record). Germination and establishment of the sown species in the single subplots were recorded first in May 2008 and ultimately in June 2010.

Characterisation of the seedling´s neighbourhood

Since it is only at the small scale of the local neighbourhood that invaders have to cope with, we recorded vegetation of 30 cm x 30 cm quadrats with the sown 10 cm x 10 cm subplots in the centres of each in summer 2008 (N= 255, figure 6 shows the radius of one vegetation relevé for one subplot sown with species mixture A as shaded quadrat). Percentage cover values of the species were recorded on a fine scale following Schmidt et al. (1974).

During the first spring after sowing (May 2008) we also recorded environmental factors that may influence establishment success at subplot level (10 cm x 10 cm): bare ground [%], cover of vegetation [%], height of vegetation [cm], cover of litter layer [%], height of litter layer [cm], cover of moss layer [%], and height of moss layer [cm]. Since direct measurements on soil characteristics and light regime on subplot level were not possible, mean weighted Ellenberg values for light and nutrients were calculated based on the vegetation relevés. Further information extracted from the relevés was the species number and evenness, proportion of legume cover, mean representation of Grimes C, S and R-strategy types, mean SLA, and canopy height of the recorded species as indicators for competitiveness of the neighbourhood.

SLA values and canopy heights of the species were extracted from the LEDA-traitbase (Knevel *et al.* 2003, www.leda-traitbase.org; Kleyer *et al.* 2008), the CSR-values were derived from the "Electronic Comparative Plant Ecology" (Hodgson *et al.* 1995) and the Ellenberg indicator values from Ellenberg (2001).

Data analyses

The current study aimed to work out biotic filtering effects of neighbouring plants on establishment chances of invading species, i.e. plot invasibility. While effects of moss and litter removal and abiotic factors on germination success were analysed in chapter 4 in more detail, we excluded plots without germination in this analysis. We rather contrasted plots with established plants at the last census versus plots where no individual survived until 2010.

Though skipping plots without germination, it was important to test if higher seedling numbers were the reason for successful establishment of the single species. Therefore, we tested the influence of seedling numbers in 2008 on final establishment success in our analyses.

Species specific analysis

Of the sown species only *Rhinanthus minor* and *Anthyllis vulneraria* had sufficient numbers of established individuals in 2010 to allow proper statistics on species level on neighbourhood effects on plot invasibility. Plot characteristics of plots with viable individuals in 2010 were tested against plot characteristics of plots where, despite successful germination, no individual was alive at the last census using Mann-Whitney U-tests. Besides the plot characteristics we tested for the effect of numbers of germinated seedlings. A significant effect of seedling numbers may indicate, that only initial seedling numbers determined on which plots individuals survived, while mortality risk may have been the same at all plots.

Analysis of general effects of neighbourhood filtering over all established species

High seedling mortality is typical for grasslands (Miles 1972; Grubb 1977; Silvertown & Dickie 1980; Kiviniemi & Eriksson 1999) and the majority of seedlings probably died through events (predation, frost heave, trampling etc.) not connected to empirically recordable plot characteristics. Nevertheless, even establishment of species only at single plots may reveal some pattern of neighbourhood selection mechanisms, if these plots stand out from the average and even if these invaded plots only differed slightly from plots, where no survival was recorded. Thus, Mann-Whitney U-Tests were performed contrasting means of plot characteristics of plots with successful establishment versus mean values of plots where no seedling survived for the eight species with viable seedlings in 2010. This study should reveal species independent general patterns of plot invasibility.

Extrinsic factors correlated with species richness

As neighbourhood species richness turned out to be strongest associated with successful invasion in our study, we also tested which of the gathered variables varied with species richness as this may contribute to the ongoing discussion on the relationship between species richness and invasibility in plant ecology (Tilman 1997; Wardle 2001; Fridley *et al.* 2007). We used Spearman correlations to examine relationships between species richness and extrinsic factors.

All statistical analyses were carried out with the program package SPSS for Windows 17.0.

Results

Establishment success

Establishment success until the third year after sowing was overall very poor for almost all species. The number of subplots, where a species germinated and where vital individuals were recorded in 2010, is given in table 14. Out of the 85 subplots that were sown with one of the three seed mixtures, 17 were occupied by one species at most (*Anthyllis vulneraria*), while of seven species out of the 15 species sown no individual survived until the last census. Therewith, the analyses were confined to eight species which occupied at least one subplot in 2010. Due to the bad establishment success and small size of the surviving individuals, neither positive nor negative interactions between seedlings within one subplot should have influenced establishment success.

Table 14: Number of plots (10 cm x 10 cm) with germination of the sown species in 2008 and number of plots out of these with successful establishment until 2010.

	number of plots		
	sown	with germination	with vital individuals 2010
Ajuga genevensis	85	15	1
Anthyllis vulneraria	85	73	17
Arabis hirsuta	85	48	1
Buphthalmum salicifolium	85	59	2
Centaurea scabiosa	85	78	4
Crepis capillaris	85	57	6
Dianthus carthusianorum	85	61	1
Rhinanthus minor	85	42	15

Seedling´s neighbourhood characteristics and establishment success

Species specific patterns of neighbourhood filtering

Plots with vital individuals of *Anthyllis vulneraria* in 2010 had significantly higher seedling numbers in 2008 ($U= 277.5$, $n_1= 56$, $n_2= 17$, $p= 0.009$). This indicated that establishment until 2010 was still influenced by initial germination success. Seedlings of *Anthyllis vulneraria* had higher establishment chances in plots with less bare ground ($U= 324.5$, $n_1= 56$, $n_2= 17$, $p= 0.046$) and with lower height of the moss cover in spring ($U= 360.5$, $n_1= 56$, $n_2= 17$,

p= 0.023). Furthermore, the proportion of legume cover was significantly lower in plots with successful establishment (U= 318, n_1= 56, n_2= 17, p= 0.039).

Plots at which *Rhinanthus minor* established until the third year after sowing (individuals in 2010= third generation) differed from those, where no establishment occurred, only in two considered factors (figure 7 and detailed in appendix 6). First, establishment was significantly better in plots with lower litter layer in spring (U= 135, n_1= 27, n_2= 15, p= 0.021). Second, highest significance reached the species number of the vegetation records describing the neighbourhood: establishment was significantly more successful in high species diversity plots (U= 71.5, n_1= 27, n_2= 15, p= 0.001).

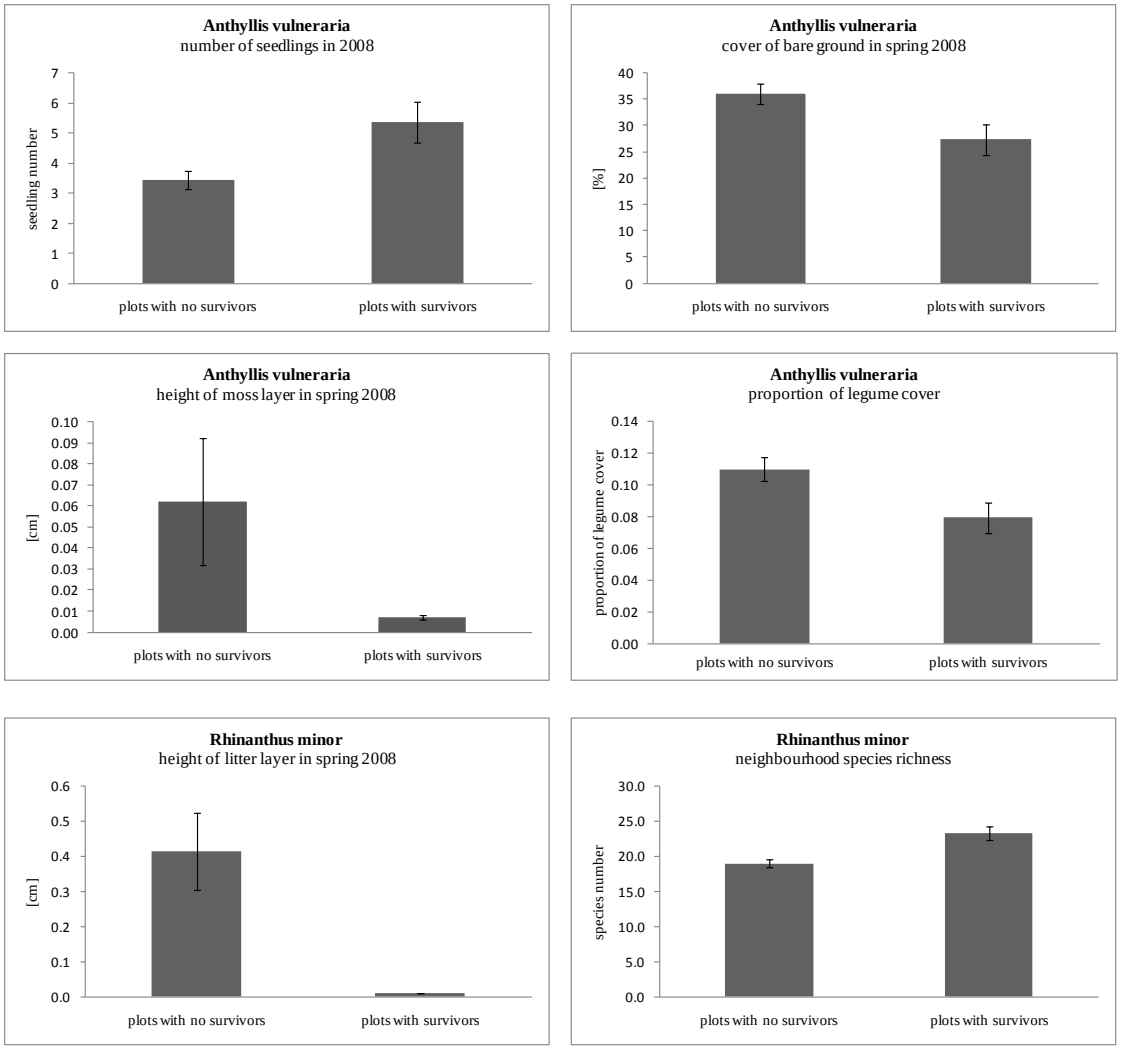

Figure 7: Means ± SE of the initial seedling numbers of *Anthyllis vulneraria* in 2008 and of neighbourhood characteristics for plots without survivors and plots with vital individuals for *Anthyllis vulneraria* (n_1= 56, n_2= 17) and *Rhinanthus minor* (n_1= 27, n_2= 15). Mann-Whitney U-tests were performed to test for significant differences between means. Only graphs for significant factors (p<0.05) are shown.

The role of neighbour species identity for establishment success of Anthyllis vulneraria and Rhinanthus minor

For both species significant differences in neighbourhood species occurrences were found (table 15). Those mostly referred to higher cover values of neighbour species in plots with establishment. Exceptions were the lower *Brachypodium pinnatum* covers (U= 421, p= 0.011) and lower *Thymus chamaedrys* covers (U= 505.5, p= 0.024) in plots with *Rhinanthus minor* establishment.

In plots with *Anthyllis vulneraria* establishment, five species reached significantly higher cover values than in plots with failed establishment (*Alchemilla monticola, Campanula rotundifolia, Cynosurus cristatus, Sanguisorba minor, Vicia sepium*).

Rhinanthus minor established in plots with higher cover values of twelve species. Four of these are listed as host species for *Rhinanthus minor* (Gibson & Watkinson 1989). However, this is also true for *Brachypodium pinnatum* which occurred with significantly lower cover in plots with establishment (U=421, p= 0.011).

The comparison of differences in neighbourhood species occurrences overlapped at least partly for the two tested species. Both species (*R. minor* and *A. vulneraria*) established better in plots with higher cover values of *Sanguisorba minor* (Rhi. min.: U= 476.5, p= 0.045, Ant. vul.: U= 282.5, p= 0.010) and of *Campanula rotundifolia* (Rhi. min.: U= 487.5, p= 0.041, Ant. vul.: U= 337.5, p= 0.050) – two stress tolerators sensu Grime.

Table 15: Mean cover values [%] of neighbourhood species are given for plots with survivors and plots without survivors of the sown species *Rhinanthus minor* and *Anthyllis vulneraria*. Arrows indicate if the cover values of neighbour species were higher or lower in the plots with survivors in comparison to the plots without survivors. Mann-Whitney U-tests were performed to test for significant differences between means. Only species which reached significant results ($p<0.05$) are listed (total species number in the relevés N= 78). Information on the CSR strategy type, if available, is given (Hodgson *et al.* 1995; Pleijel & Danielsson 1997; Dumont *et al.* 2009) and *Rhinanthus minor* hosts identified in literature (Gibson & Watkinson 1989) are indicated.

			Rhinanthus minor			*Anthyllis vulneraria*		
	Grime´s strategy type	host	plots without survivors n= 27		plots with survivors n=15	plots without survivors n= 56		plots with survivors n=17
Agrostis tenuis	CSR	yes	3.0	↗	5.5			
Alchemilla monticola						0.0	↗	0.5
Brachypodium pinnatum	SC	yes	20.3	↘	4.5			
Campanula rotundifolia	S		0.5	↗	0.9	0.6	↗	1.5
Cerastium holosteoides			0.0	↗	0.0			
Cynosurus cristatus	CSR	yes				0.4	↗	1.3
Festuca pratensis	CSR		1.0	↗	2.3			
Festuca rubra	CSR	yes	2.7	↗	6.8			
Hieracium pilosella	S/CSR	yes	1.3	↗	2.8			
Plantago lanceolata	CSR	yes	6.6	↗	9.0			
Potentilla heptaphylla			0.1	↗	0.4			
Potentilla tabernaemontani			0.8	↗	1.6			
Ranunculus bulbosus	SR		0.2	↗	0.3			
Sanguisorba minor	S		3.8	↗	7.4	2.5	↗	6.0
Scabiosa columbaria	S/SR		0.6	↗	3.8			
Thymus chamaedrys			0.4	↘	0.2			
Vicia sepium						0.0	↗	0.8

General effects of neighbourhood filtering over all established species

Some general patterns on plot characteristics separating plots with successful invasion from plots with establishment failure could be revealed (figure 8 and detailed in appendix 7). Highest significance reached the higher species diversity of plots with successful invasion. Height of litter layer tended to be lower over all species in invaded plots, as it had been shown in the single species analysis on *Rhinanthus minor* establishment.

Also height of vegetation in spring was significantly lower in successfully invaded plots.

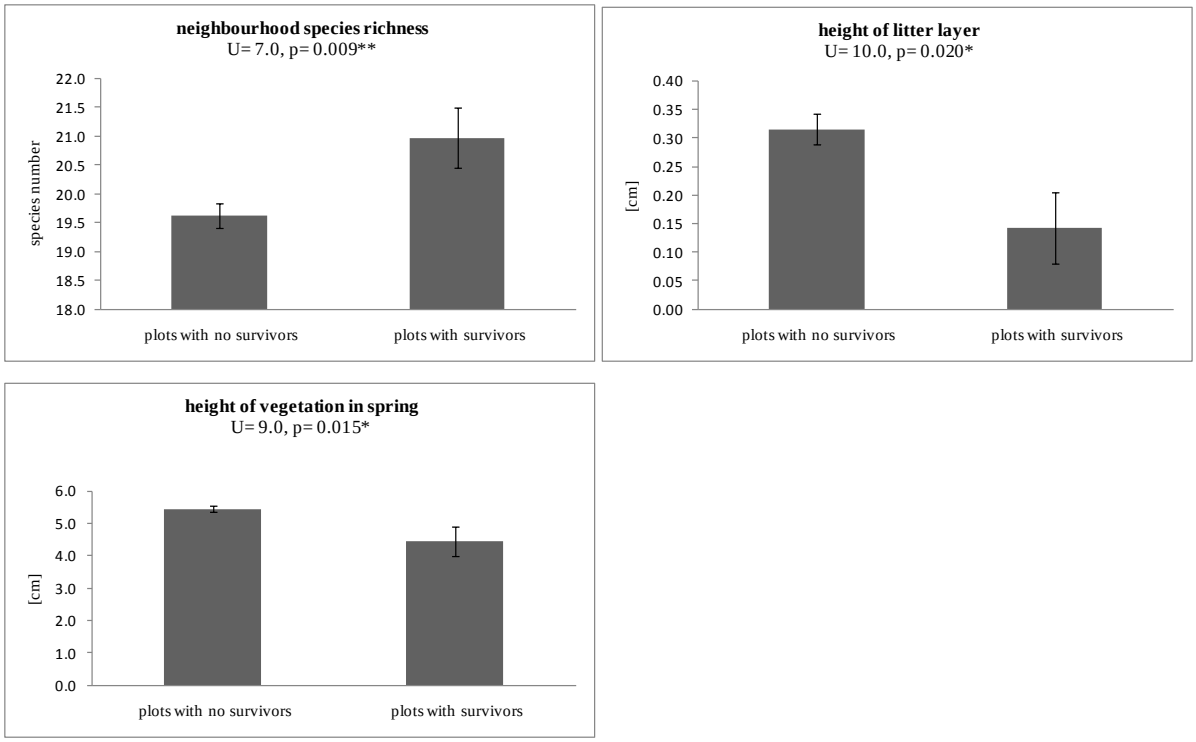

Figure 8: Means ± SE of neighbourhood characteristics for plots with and without survivors. Mann-Whitney U-tests were performed to test for significant differences between means of neighbourhood characteristics of plots with survivors versus plots without vital individuals of eight species. Only graphs for significant factors ($p<0.05$) are shown.

Extrinsic factors correlated with species richness

As species diversity turned out to be most important for plot invasibility in the single species analysis of *Rhinanthus minor* as well as in the analysis performed over all eight established species, extrinsic factors correlated with species richness were analysed (table 16).

Strongest correlation was found between species richness and eveness ($\rho= 0.725$, $N= 255$, $p= 0.000$). Thus, dominance of single species tended to be more uncommon the higher the species diversity was.

Furthermore, higher species richness came along with higher summed up cover values of recorded species ($\rho= 0.417$, $N= 255$, $p= 0.000$).

Next, stress strategists sensu Grime reached higher cover values the higher the species richness was ($\rho= 0.331$, $N= 255$, $p= 0.000$), while competitors ($\rho= -0.257$, $p= 0.000$), as well as ruderals ($\rho= -0.290$, $N= 255$, $p= 0.000$), declined.

Mean Ellenberg values for nutrients also declined with increasing species richness ($\rho= -0.293$, $N= 255$, $p= 0.000$).

Furthermore, weak but significant positive correlations were revealed between species richness and cover ($\rho= 0.247$, $N= 255$, $p= 0.000$) and height of moss layer ($\rho= 0.137$, $N= 255$,

p= 0.029), while the correlation with vegetation height in spring was negative (ρ= -0.173, N= 255, p= 0.006).

Finally, mean weighted SLA of the neighbourhood species showed a weak but significant negative correlation with species diversity (ρ= -0.127, N= 255, p= 0.042).

Table 16: Spearman correlations between species richness and neighbourhood characteristics over all sown plots (N= 255). p<0.05=*, p<0.01=, p<0.001=***.**

	Spearman's rho	correlation coefficient	p value
spring measurements	**height of vegetation**	**-0.173**	**0.006 ****
	cover of vegetation	0.052	0.412 n.s.
	cover of moss layer	**0.247**	**0.000 *****
	height of moss layer	**0.137**	**0.029 ***
	cover of litter layer	-0.019	0.764 n.s.
	height of litter layer	-0.089	0.155 n.s.
	bare ground	-0.100	0.110 n.s.
summer measurements	**sum of species cover values**	**0.417**	**0.000 *****
	height of vegetation	**0.131**	**0.037 ***
Grime´s strategy type	Ellenberg L	-0.114	0.069 n.s.
	Ellenberg N	**-0.293**	**0.000 *****
	proportion cover of legumes	0.017	0.784 n.s.
	eveness	**0.725**	**0.000 *****
	C	**-0.257**	**0.000 *****
	S	**0.331**	**0.000 *****
	R	**-0.290**	**0.000 *****
community weighted means	canopy height	-0.103	0.100 n.s.
	SLA	**-0.127**	**0.042 ***

Discussion

Seedling´s neighbourhood characteristics and establishment success

Establishment success

Final invasion success of all species was rather poor irrespective of the taken criteria (seedling numbers or successfully invaded plots (appendix 5, table 14 respectively)). Such high seedling mortality is common in closed grassland swards (Miles 1972; Grubb 1977; Silvertown & Dickie 1980; Kiviniemi & Eriksson 1999). A multitude of factors besides direct or indirect neighbourhood influences might have led to death of the individuals. These factors may be physical hazards and pathogens, herbivores or desiccation (Harper 1977; Ryser 1993;

Hutchings & Booth 1996a). In general, seedlings live under severe stress in closed grassland swards and the vast majority of seedlings stays very small even over years and dies without ever producing seeds (Miles 1972; Harper 1977; Silvertown & Dickie 1980; Stampfli & Zeiter 1999).

That just *Rhinanthus minor* and *Anthyllis vulneraria* out of the sown species were most successful after three years may be due to the fact that short lived species generally rely more on generative regeneration and therefore should be more successful in sowing experiments than long-lived species (Milberg 1994a, b).

Species specific patterns of neighbourhood filtering

At the end of the study only two of the sown species were represented by enough individuals to allow a statistical comparison of plots with successful establishment versus plots at which all individuals had died.

Rhinanthus minor was the only successful strict (summer-)annual species. Therewith, individuals in 2010 represented the third generation. In contrast, individuals of *Anthyllis vulneraria* belonged to the first generation and only flowered by the majority in 2010. *Anthyllis vulneraria* belongs to the facultatively polycarpic perennials which are often polycarpic but monocarpic under certain conditions (Sterk 1975). Ehrlen and Lehtilä (2002) classified *Anthyllis vulneraria* as a semelparous species (monoecy or dioecy) with an average lifespan of 4.3 years.

The different life histories of these two species may also explain differences in neighbourhood effects.

For *Anthyllis vulneraria* the number of seedlings in the first year after sowing still made an impact on the occupation chance of a sown plot at the end of the study. Thus, as the living individuals represented the first generation, neighbourhood influences may have been largely confined by the fact that higher initial seedling numbers raised the chance that at least one individual survived until the last census. Therewith, the study period was probably too short for more precise neighbourhood filtering effects to emerge.

Nevertheless, occupied plots had less bare ground and a lower moss layer than plots at which all seedlings died. That regeneration of *Anthyllis vulneraria* is not strictly limited by gaps has also been found by Verkaar et al. (1983b), what was in accordance with the higher survival at plots with less bare ground in our study – but contradictory to Grubb (1976; 1977) who stated that short lived species only regenerate in gaps.

Furthermore, small but significant differences between the proportion of legume cover of plots with and without establishment of *Anthyllis vulneraria* were revealed. Plots with establishment had less cover of other legumes. This result confirmed the result of a study on plot invasibility by legumes dependent on the resident species: legumes were found to be more successful at invading plots occupied by grasses and non-leguminous forbs, than those plots occupied by legumes (Turnbull *et al.* 2005).

For *Rhinanthus minor* the occupied plots in 2010 were colonized by the third generation and therefore were filtered out over three years as being appropriate for germination and finally setting seeds. Higher species diversity of occupied plots reached highest significance in the comparison of the plots where *Rhinanthus minor* went extinct until 2010 versus the plots with successful establishment until 2010. Studies performed in natural systems often found higher establishment success in higher diversity plots (reviews: Prieur-Richard & Lavorel 2000; Wardle 2001; Fridley *et al.* 2007). The possible links between species richness and invasion success are discussed in a separate section in the following discussion.
The occupied plots also stood out by a lower litter layer in spring. Due to the annual life cycle of *Rhinanthus minor* appropriate germination conditions should be of major importance. The inhibition of seedling emergence and survival through litter has been shown by several studies (Fowler 1988; Hurst & John 1999; Emery & Gross 2006) and also seemed to apply to the *Rhinanthus minor* pattern in our study.

The role of neighbour species identity for establishment of Anthyllis vulneraria and Rhinanthus minor

The analysis of links between single species covers in the neighbourhood and invasion success showed that invasion was successful in plots where specific species occurred with higher cover values. However, it should be pointed out, that those species cover values in invaded plots were still below 10 %.
The only clear exception of this pattern was the significantly lower cover values of *Brachypodium pinnatum* in plots with *Rhinanthus minor* establishment. According to former studies *Brachypodium pinnatum* has detrimental effects on forbs as it produces a dense litter layer and also contributes to raising nitrogen levels within stands (Bobbink & Willems 1987; Hurst & John 1999). This combination may explain the negative impact on *Rhinanthus minor* establishment. As *Rhinanthus minor* needs germination niches in spring, litter produced by *Brachypodium pinnatum* during winter may have hampered germination. Additionally, as

hemiparasitic plant *Rhinanthus minor* loses its advantage when nutrient levels are higher, while other species may gain competitive strength.

A further hint for the importance of the hemiparasitic life strategy of *Rhinanthus minor* for its establishment pattern might have been that four of the species with higher cover at occupied plots are listed as *Rhinanthus minor* host species (*Agrostis tenuis, Festuca rubra, Hieracium pilosella, Plantago lanceolata*) (Gibson & Watkinson 1989). However, this is also true for *Brachypodium pinnatum*. Maybe the other mentioned characteristics of *Brachypodium pinnatum* level out the advantage of having *Brachypodium pinnatum* available as a host.

Agrostis tenuis, one of the *Rhinanthus minor* host grasses with higher cover in invaded plots, has also been found to offer generally good conditions for seedling survival in a study performed by Turkington (1979) on the hospitality of swards dominated by the different grass species to transplants.

Anthyllis vulneraria established in plots where five species were more frequent than in the plots where all seedlings died. One of these species was *Cynosurus cristatus*, which has also been found to offer best conditions for the survivorship of another legume (*Trifolium repens*) in comparison to neighbourhoods dominated by other grasses (Turkington *et al.* 1979).

In this former study by Turkington et al. (1979) the authors distinguished between hospitable and aggressive neighbours, while responsible traits or mechanisms for this distinction were left open.

Also more subtle mechanisms behind higher cover values of specific species at plots with higher invasion success may be possible. For example, Harper (1957) described that *Ranunculus bulbosus,* which also reached higher covers in plots with *Rhinanthus minor* invasion, appears to protect neighbouring plants from herbivory due to the possession of an unpleasant glycoside (Ranunculin).

Vicia sepium reached higher cover values in plots occupied by *Anthyllis vulneraria*. According to Hodgson et al. (1995) the main habitat of *Vicia sepium* are soil heaps, which may be created by moles or ants. *Anthyllis vulneraria,* as well as *Rhinanthus minor,* established more often in plots with higher *Campanula rotundifolia* and *Sanguisorba minor* covers. These species were the only absolute stress strategists sensu Grime within the group of species with significant results in this study. *Sanguisorba minor* was found to best establish in grassland gaps versus tufts (Ryser 1993). These facts indicated a preference for disturbed plots for these two species. Thus, higher occurrence of these neighbour species at invaded plots may imply higher germination and establishment niche availability. The higher cover of stress strategists may further indicate that the plots suitable for successful invasion

represented special microsites with less competitive surrounding as higher stress levels indicate a limitation of the rate of dry matter production (Grime 1979). This limitation could be caused by a multitude of external constrains, like shortages or excesses in the supply of solar energy, water or mineral nutrients (Grime 1979). Lower cover of *Brachypodium pinnatum* may at least indicate lower nutrient levels at the invaded plots.

Overall, these results suggested that it was not the dominance of single competitive species in the surrounding that restricted the invasion success of the two species (with exception of *Brachypodium pinnatum* cover for *Rhinanthus minor*). Other studies concluded that it was mainly the dominance of single species that prevented species invasion (Wardle 2001; Smith *et al.* 2004; Emery & Gross 2006). Rather, the co-occurrence of less competitive species indicated that invasion was most likely on spots with higher stress levels, allowing co-existence of many competitive weak but stress tolerant species.

General effects of neighbourhood filtering over all established species

In the analysis over all sown species height of vegetation and litter layer in spring were significantly lower at successfully invaded plots.

Litter is known to have profound effects on community structure by reducing germination as well as establishment (Silvertown 1980b; Eriksson 1995) and fitness of established plants (Facelli & Pickett 1991).

Lower height of vegetation in spring may offer good light conditions which could enhance the invader fitness, especially as light has been shown to be often the most important limiting resource in grassland determining species occurrence (Hautier *et al.* 2009).

However, the most striking difference between successfully invaded plots versus plots where all seedlings died, was the higher species richness of the invaded plots.

Species richness and invasibility

As well the general analysis over all species, as the analysis on *Rhinanthus minor* establishment patterns, showed a preference for higher establishment at plots with higher species richness. This result fits into the discussion on the effects of plant diversity on invasibility (see box 2). Therefore, we wanted to elucidate the role of diversity for plot invasibility for our study system and looked for parameters co-varying with diversity.

Species richness on the neighbourhood scale was strongly positively correlated with evenness. Therewith, higher species richness came along with balanced species cover distributions and thus without dominance of single species. This result was in accordance with Wardle´s (2001)

suggestion that the abundance of a potentially dominant species should affect plot invasibility. Declining invasion success with increasing dominance of single species in our study could be credited to the effects of the dominant species on productivity, light or litter (Smith & Knapp 1999; Wardle 2001). As species becoming dominant in grasslands are usually the more competitive ones, higher evenness already pointed to a less competitive environment in species rich plots.

This was approved by the correlations of species richness with Grime´s strategy types. Higher species richness was correlated with lower cover values of species belonging to the competitor and the ruderal strategy groups. In contrast, stress tolerators were more common the higher the species diversity of the plots was. As stress tolerators are usually slow growing species, the weak negative correlation of species diversity with mean SLA and height of vegetation in spring might be attributed to higher covers of stress strategists.

Low vegetation in spring further should come along with higher light availability at the beginning of the growing season. As light limitation is a crucial factor limiting species co-occurrence in grassland (Hector *et al.* 2001; Hautier *et al.* 2009), this low vegetation height in spring should also have promoted growth and survival of seedlings and juveniles of the invaders.

Why the species rich plots limited the abundance of potentially dominant species and promoted stress strategists may only be speculated. Stress, disturbance or a combination of both factors limit the expression of dominance and therewith allow plants of smaller stature to co-exist with strong competitors and therewith increase local species richness (Grime 1979).

A stressful environment is mostly created by limitations or excesses of light, water or nutrients (Grime 1979). One hint that at least nutrient limitation may have contributed to the more stressful environment of the higher diversity plots in our study, was the significant negative correlation between species richness and mean Ellenberg indicator values for nutrients.

Therewith, species diversity seemed to be higher in plots with specific - basically more stressful - conditions. The importance of such special sites within grassland swards was also found by Peart (1989). Invasion of closed swards in perennial vegetation was close to zero in average plots but limited to unusually low biomass plots with higher light intensity in his study. High diversity plots in our study tended to have more and higher moss layer. This, together with the significantly lower vegetation height in spring, may indicate higher light availability at species rich plots in our study as well, though this has not been indicated by higher Ellenberg values for light.

Furthermore, moss cover can have direct positive effects on seedling survival, though it hampers germination of most species (Keizer *et al.* 1985). Moss layer was significantly positively correlated with species diversity in our study. However, in the single species analysis *Anthyllis vulneraria* showed significantly better establishment in plots with lower moss cover. Thus, our results indicated, that moss layer was none of the co-varying extrinsic factors with positive impact on invader establishment.

The results supported the hypothesis that higher small scale species richness promotes invasibility – due to the fact that diversity itself was a result of factors that, by the majority, promoted invasibility in our system and maybe also due to facilitative effects.

The reverse relationship found in other, often experimental studies (Knops *et al.* 1999; Levine 2000; Kennedy *et al.* 2002; Knight & Reich 2005), could not be validated.

This suggested, that though species diversity per se may have negative effects on invasibility when co-varying factors are absent in experimental studies (due to niche separation or sampling effects), these effects are overridden by the factors that are linked to higher diversity in natural systems.

Conclusion

It was our intention to filter out neighbourhood effects on invasion success in a natural ecosystem. Despite very high seedling mortality of all sown species - probably mostly due to a vast number of neighbourhood independent mortality causes - some patterns of neighbourhood filtering mechanisms could be revealed.

We found hints for facilitation playing a role: host species occurrence and maybe even protection from herbivory by other species could have influenced *Rhinanthus minor* establishment. A legume tended to establish more successfully in plots with less cover of other legumes. Also, the survival of all species tended to be higher in plots with higher species richness. On the one hand this could also point to the importance of facilitative effects as higher species richness might raise the chance of a species being present which facilitates invasion (Levine & D'Antonio 1999). On the other hand higher species richness was correlated with a number of other plot characteristics mainly pointing to a less competitive environment at plots with better establishment. Therewith, our study supported the positive relationship between diversity and invasibility giving hints for the “diversity begets diversity” hypothesis as well as for the perception that diversity and invasibility were results of co-varying extrinsic factors.

It is generally assumed that neighbourhood effects were only weak and hard to grasp in natural systems due to a high fraction of randomness involved in community assembly (Ryser 1993; Shipley 2010). However, that those patterns of neighbourhood effects emerged in our study despite the poor establishment success and therewith poor data basis, may indicate that quite subtle mechanisms are involved in small scale assembly processes and detectable even in a natural system.

Nevertheless, the impact of the single factors for assembly processes has to be put to test in further experiments to verify or neglect the hints found for neighbourhood selection mechanisms.

Chapter 6

Land use history, functional traits and biotic filter – which factors cause indicator species status in ancient and recent calcareous grasslands?

Abstract

While ancient calcareous grasslands suffered strong decreases since the 19th century, unprofitable arable fields were also turned back into grasslands due to no profitability. Many studies found that even after decades and with species-rich ancient grasslands close-by, those recent grasslands on ex-arable fields do not resemble the species composition of ancient sites.
We extracted indicator species of adjacent ancient and recent grasslands with comparable abiotic conditions and analysed reasons for the restricted occurrence of indicator species. We asked which functional traits make the indicator species stand out from the species pool and also questioned the role of biotic filtering for species failure in the other grassland type.
Indicator species of recent grasslands were competitive species adapted to higher nutrient availability and often introduced to the former arable fields by humans as crop or arable weed. Hence, they might have persisted at recent sites since the end of agricultural use despite changes in abiotic conditions.
Indicators of ancient grasslands were small species with specific requirements for germination and establishment. Comparisons of community weighted means for functional traits that separated the indicators from the species pool showed significant differences between ancient and recent grasslands. Our results suggested that indicators of ancient sites might have failed at recent sites due to higher competitive environment and thus biotic filtering.

Introduction

Millennia of traditional management created the rural landscapes of Northwestern Europe. Therewith, calcareous grassland habitats evolved with an exceptionally high small-scale species richness of vascular plants (Willems 1990; van der Maarel & Sykes 1993; WallisDeVries *et al.* 2002), which puts them into the focus of conservation efforts today. Due to altered farming practices those grasslands are suffering decreases since the 19th century

with strongest declines during the 1960s and 1970s (Karlík & Poschlod 2009). Simultaneously, since mid of the 20th century intensification of agriculture led to abandonment of former arable fields, especially at agriculturally less favourable sites (Baumann *et al.* 2005; Mailänder 2005). These former arable fields were often turned back into grasslands, either by natural succession and subsequent management by grazing or hay making, or by the incorporation of seeds via hay application.

Therewith, actual calcareous grassland landscapes comprise ancient grasslands with long continuity of grazing and recent grasslands which developed from former arable-fields (Baumann *et al.* 2005; Mailänder 2005). Several studies showed that irrespective of the connectivity between recent and ancient grasslands, whether hay-seeds were introduced after abandonment or not and irrespective of the age of recent grasslands, species composition of recent grasslands may converge towards ancient sites, but never resemble it completely (Dzwonko & Loster 1998; Cousins & Eriksson 2002; Pywell *et al.* 2003; Lindborg & Eriksson 2004; Lepš *et al.* 2007; Fagan *et al.* 2008).

Striking is the failure of single species typical for ancient grasslands to establish at the recent sites (Lindborg & Eriksson 2004; Fagan *et al.* 2008). However, also species more or less exclusively present at restored sites were pointed out (Poschlod *et al.* 2008; Karlík & Poschlod 2009).

The same pattern has been found for species composition at ancient and secondary forests and the reasons for this were analysed in several studies (Peterken 1974; Graae & Sunde 2000; Mabry *et al.* 2000; Butaye *et al.* 2001; Dzwonko 2001; Bellemare *et al.* 2002; Jacquemyn *et al.* 2003b; Verheyen *et al.* 2003; Graae *et al.* 2004; Wiegmann & Waller 2006; Vojta 2007).

Studies found one explanation for the failure of some species of ancient grasslands and ancient woods in dispersal limitation (Bonn & Poschlod 1998; Poschlod *et al.* 1998; Hermy *et al.* 1999; Dzwonko & Loster 2007).

Furthermore, abiotic conditions, mainly higher fertility of secondary sites, helped to explain differences in species composition in many studies (e.g. Walker *et al.* 2004). Nevertheless, restoring soil conditions often failed to result in successful restoration of former plant species richness (Berendse *et al.* 1992; Pfadenhauer & Klötzli 1996; Bakker & Berendse 1999).

Also former land-use could explain actual species distribution independent from environmental differences to some extent (Butaye *et al.* 2001; Chýlová & Münzbergová 2008; Karlík & Poschlod 2009). The origin of exclusive occurrences of some indicators for secondary grasslands was further found in former cultivation of species like *Onobrychis*

viciifolia (Karlík & Poschlod 2009) now named a characteristic calcareous grassland species (Oberdorfer 2001).

Nevertheless, explanations for the importance of the history of the sites for species composition beyond dispersal and environmental conditions (including actual management) are largely missing.

The importance of functional traits for species failure or successful establishment at secondary grassland and woodland sites has been studied in the last years (Dzwonko 2001; Fagan *et al.* 2008). The conclusion of studies focusing on characteristics of species which did not or poorly establish at recent grasslands or woods was, that these were often rare and threatened species associated with infertile soils and typical for the respective habitat, while generalist species were quite successful at secondary habitats (Dzwonko 2001).

So far the biotic environment has been neglected as explanation for indicator species distribution between ancient and recent grasslands, although it may give an additional hint for explaining actual occurrences of species. It is long known that not only the abiotic but also the biotic environment has an impact on establishment success and thus vegetation composition. The influence of the neighbourhood on germination and seedling development has been discussed and demonstrated (Platt 1975; Grubb 1977; Gross & Werner 1982; Kennedy *et al.* 2002; Emery & Gross 2006). It has been pointed out that not the presence of single species should be important for establishment success, but the dominant species identity (Wilson & Gitay 1995a; Wardle 2001; Emery & Gross 2006) or more precise, the dominant functional group (Goldberg & Werner 1983b; Emery 2007).

The current study is based on a study of Karlik & Poschlod (2009) who showed that for the vegetation composition in several ancient and recent grasslands of the nature reserve “Kaltes Feld” the abiotic filter plays a minor role for vegetation composition in comparison to the landuse-history.

We went for a functional trait approach also questioning the importance of biotic filtering for restricted occurrences of indicator species.

The idea was that if certain trait attributes are over represented among indicator species, this may indicate that these traits cause the restricted occurrence of these species. Thus, we first wanted to know which plant functional traits or strategies make the indicators stand out from the residual species pool of the site, to get an idea which mechanisms and processes might be important to get the indicator species status.

Furthermore, we compared community weighted means of those traits at the communities where target species occur with those of the sites where those species do not succeed, to assess the role of the biotic filter for restricted species occurrences.

We aimed to answer following questions:

(1) Which traits make a species an indicator for ancient and recent grasslands, respectively?
(2) Can the biotic environment, described by dominating functional traits, help to explain the restricted occurrences of indicator species?

Methods

Study site

The study area was the nature reserve "Kaltes Feld" which is located in the central part of the Swabian Alb in south-western Germany (586 - 699 m NN, annual precipitation 1050 mm, mean temperature 7 °C). Soils at the investigated calcareous grasslands within this nature reserve are shallow (approx. 6 cm – 38 cm). The age of the single fields within this area was determined using cadastre maps from 1830 and land-use maps from 1953 and 2002 (Mailänder 2005). Grasslands continuously marked as pastures since 1830 were considered as ancient grasslands. Recent grasslands were marked as arable land in one of the older maps (from 1830 or 1952) and as grasslands at least on the most recent map (from 2002). Vegetation data from ten ancient and eight recent grasslands were available. The recent grasslands can be divided into old grasslands with last agricultural use 55 to 150 years ago and young grasslands that are only 50 to 60 years old.

Vegetation data

We took vegetation data of those ancient and recent grasslands of a study conducted by Karlik & Poschlod (2009). One area, which was included in this former study by Karlik & Poschlod (2009), had significant divergent abiotic conditions from the other areas and was therefore excluded from our study.
On each of the 10 ancient and 8 recent sites vegetation was sampled on five 2m x 2m plots placed semi-randomly (exclusion of rock, bush and strongly disturbed patches) in each grassland according to Braun Blanquet´s (1964) nine grade abundance dominance scale.

Environmental data

For each plot following soil physical and chemical parameters were measured: soil depth, water holding capacity (WHC), pH (H2O), pH (CaCl2), conductivity, potassium (K) and phosphorus (P). Further information was available on altitude, inclination, exposition and potential direct solar radiation on each plot (calculated from data on altitude, inclination and exposition; for details see Karlik and Poschlod (2009)).

Plant trait data

For all species included in the vegetation records of both types of grasslands, we collected information on functional traits which were extracted from the databases LEDA (Knevel *et al.* 2003, www.leda-traitbase.org; 2008), BIOPOP (Jackel *et al.* 2006, www.floraweb.de/proxy/biopop/de/index.php), Diasporus (Bonn *et al.* 2000) and CloPla3 (Klimešová & de Bello 2009, http://clopla.butbn.cas.cz) (table 17). Besides these basic traits we also included some widely available generic classifications: the Ellenberg indicator values (Ellenberg *et al.* 2001), Grimes´ CSR-stragegy classification (Electronic Comparative Plant Ecology (ECPE), Hodgson *et al.* 1995), the non-legume/legume distinction and the herb/grass distinction.

Data analyses

All analyses were performed with herbal species only, excluding shrubs and trees. Traits were only available on the adult stages of shrubs and trees that vastly do not have to compete with the herbaceous layer. Mixing up the traits of different vegetation layers would have complicated to find the traits conferring indicator species status or describing the biotic environment at the different sites.

Table 17: Plant functional traits and classifications included in the analyses. Trait units, data sources and percentage of missing values are given. Data sources: LEDA (Kleyer *et al.* 2008), BIOPOP (Jackel *et al.* 2006), ECPE="Electronic Comparative Plant Ecology"(Hodgson *et al.* 1995), CloPla3 (Klimešová & Klimes 2008; Klimešová & de Bello 2009), Ellenberg indicator values (Ellenberg *et al.* 2001), Diasporus (Bonn *et al.* 2000).

	scale	% missing values	data source
seed number	metric	27	LEDA
terminal velocity	metric	11	LEDA
number of dispersal vectors	metric	7	Diasporus
anemochorous dispersal	yes/no	7	Diasporus
zoochorous dispersal	yes/no	7	Diasporus
epizoochorous dispersal	yes/no	7	Diasporus
endozoochorous dispersal	yes/no	7	Diasporus
hemerochorous dispersal	yes/no	7	Diasporus
seed mass	metric	5	LEDA
germination season	spring, all year, autumn	5	BIOPOP
minimum germination temperature	metric	47	BIOPOP
maximum germination temperature	metric	43	BIOPOP
seed dormancy	no, no/physiological, physiological, physical	43	BIOPOP
canopy height	metric	0	LEDA
leaf distribution	rosette, semi-rosette, regularly	0	LEDA
specific leaf area (SLA)	metric	2	LEDA
leaf dry matter content (LDMC)	metric	11	LEDA
minimum connection to mother plant	1-2 years, > 2 years	11	LEDA
lifespan	short / long	0	LEDA
seedbank longevity index	metric	3	LEDA
leaf phenology	vernal, aestival, partly evergreen, evergreen	0	BIOPOP
woodiness	non-woody, semi-woody, woody	0	LEDA
number of budbank-layers	metric	5	CLOPLA3
maximum lateral spread per year	< 100 mm, 100-250 mm, > 250 mm	1	CLOPLA3
earliest month of seed shedding	metric	3	LEDA
latest month of seed shedding	metric	3	LEDA
seed shedding duration	metric	3	LEDA
Ellenberg indicator value for light	ordinal	3	Ellenberg
Ellenberg indicator value for moisture	ordinal	21	Ellenberg
Ellenberg indicator value for reaction	ordinal	26	Ellenberg
Ellenberg indicator value for nitrogen	ordinal	13	Ellenberg
grass (or herb)	yes/no	0	-
non-legume (or legume)	yes/no	0	-
growth form	therophyte, hemicryptophyte, geophyte, chamaephyte, liana	0	LEDA
% C Crime	0-100 %	41	ECPE
% S Grime	0-100 %	41	ECPE
% R Grime	0-100 %	41	ECPE

Importance of environmental factors for vegetation composition

To evaluate the importance of environmental factors for differences in species composition at ancient and recent grasslands, we conducted a PCA of the vegetation data and correlated all available environmental data and the factor history of the vegetation relevés with the axes, setting the cut-off value for correlation with the ordination axes at 0.4 (PCORD5, McCune &

Mefford 1999). Prior to ordination Braun Blanquet values were transformed to percentage cover values using the mean percentage value of each class. The use of PCA was indicated since length of gradient in the DCA analysis was less than 3 S.D. (ter Braak & Šmilauer 2002).

Indicator species analysis

To identify species that are typically found in grasslands of a certain age, we used the indicator species analysis according to Dufrene and Legendre (1997), as available in the R-package labdsv (Roberts 2006). The method is applicable to groups of different sample size and combines information on the concentration of species abundance in a particular group of samples and the faithfulness of occurrence of a species in that group. It produces indicator values for each species in each group, which are tested for statistical significant differences using 10.000 iterations of randomization to calculate probabilities. As groups we distinguished between all plots of the ancient grasslands and plots from recent secondary grasslands (old and young grasslands).

Plant functional traits separating indicator species from the species pool

We wanted to identify traits that may cause the status as indicator species. Thus, we compared trait attribute distributions for categorical traits in the indicator species groups with trait distributions within the remaining species groups of the respective species pools (= all other species appearing in the vegetation records of this study) using Chi^2-tests.
Accordingly, we tested for significant differences between mean trait values of the indicator species and mean trait values of the remaining species of the species pool for quantitative traits with Mann-Whitney U-tests.

Biotic environment at recent and ancient grasslands

To define the biotic environment of each plot, we calculated community weighted means using the FD package in R (Laliberté & Shipley 2010) for all traits that separated indicator species from the species pool. All traits were not available for every species (table 17). For categorical traits we calculated the relative abundance of each trait attribute.

Results

Importance of environmental factors for vegetation composition

The PCA (figure 9) showed that none of the environmental factors related to soil fertility, pH, hydrology etc. could explain variation in vegetation composition of the study area. The only strong correlation with the first two axes was found for the factor history. Thus, the history and therewith time since last agricultural use was the best explanatory variable for differences in vegetation composition and separated grasslands of decreasing age along the first two axes.

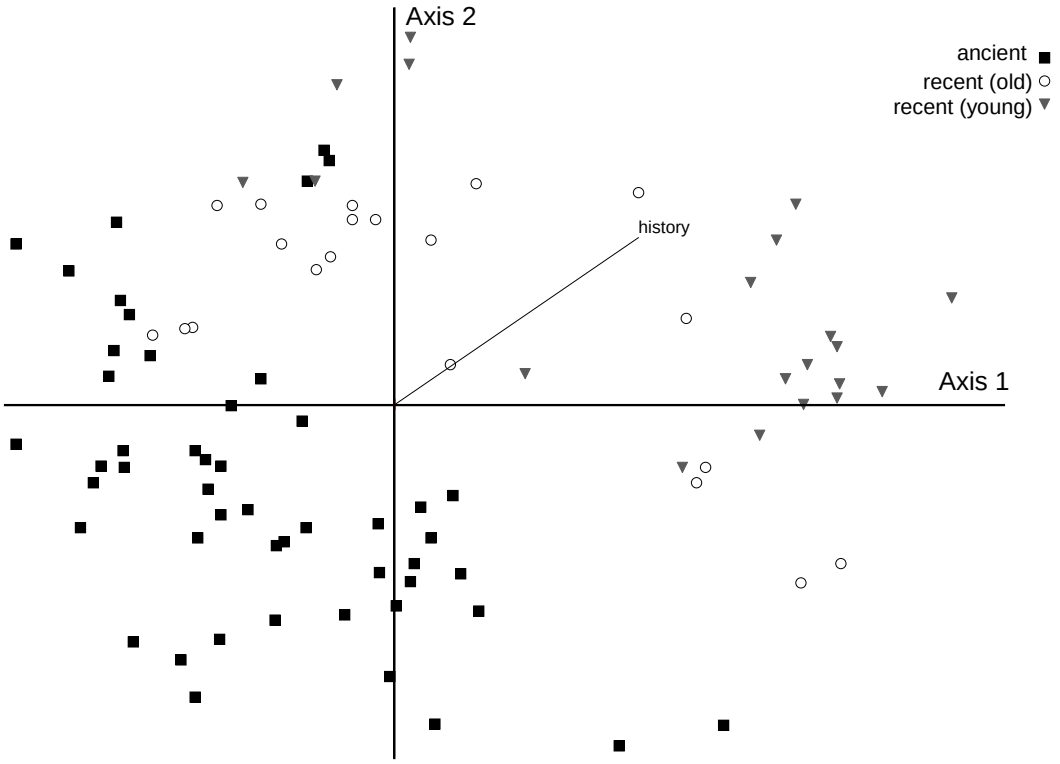

Figure 9: PCA of vegetation relevés of ancient and recent grasslands and overlay of correlations of environmental factors of single plots with the axes. Cut-off value for correlations of environmental factors with axes: r^2>0.4. Axis 1 explains 23.08 % and axis 2 explains 16.25 % of variance.

Indicator species analysis

The indicator analysis identified 17 indicator species for ancient grasslands and 40 indicator species for recent grasslands (table 18). Ancient grassland species were mainly basi- and calciphilous grassland species such as *Carex flacca*, *Hippocrepis comosa* and *Scabiosa columbaria*. In contrast, indicators of recent grasslands were many mesophilous species such as *Avenula pubescens*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Trisetum flavescens*, *Trifolium pratense*, *Veronica chamaedrys* and several arable weeds and ruderals.

Table 18: Results of the indicator species analysis according to Dufrene and Legendre (1997). Indicator species of ancient and recent grasslands and their indicator values are given (only species are shown with p<0.05).

species	cluster	indicator value	probability
Aster amellus	ancient	0.12	0.046
Briza media	ancient	0.60	0.001
Carduus acanthoides	ancient	0.40	0.022
Carex caryophyllea	ancient	0.68	0.000
Carex flacca	ancient	0.58	0.010
Carlina vulgaris	ancient	0.48	0.000
Cirsium acaule	ancient	0.71	0.000
Euphorbia verrucosa	ancient	0.13	0.047
Gentiana verna	ancient	0.08	0.037
Hieracium pilosella	ancient	0.42	0.000
Hippocrepis comosa	ancient	0.80	0.000
Leontodon hispidus	ancient	0.52	0.012
Linum catharticum	ancient	0.53	0.031
Polygala amarella	ancient	0.21	0.045
Potentilla tabernaemontani	ancient	0.47	0.015
Prunella vulgaris	ancient	0.53	0.001
Scabiosa columbaria	ancient	0.54	0.017
Achillea millefolium	recent	0.52	0.024
Agrimonia eupatoria	recent	0.55	0.000
Ajuga genevensis	recent	0.05	0.000
Allium oleraceum	recent	0.08	0.000
Arabis hirsuta	recent	0.12	0.033
Arenaria serpyllifolia	recent	0.13	0.000
Arrhenatherum elatius	recent	0.30	0.000
Astragalus glycyphyllos	recent	0.05	0.000
Avenula pubescens	recent	0.18	0.003
Bromus erectus	recent	0.57	0.012
Centaurea scabiosa	recent	0.15	0.007
Cerastium arvense	recent	0.08	0.000
Cerastium fontanum	recent	0.13	0.018
Convolvulus arvensis	recent	0.20	0.001
Cynosurus cristatus	recent	0.08	0.000
Dactylis glomerata	recent	0.38	0.001
Festuca pratensis	recent	0.17	0.005
Galium album	recent	0.30	0.003
Galium verum	recent	0.21	0.022
Hypericum perforatum	recent	0.36	0.002
Linaria vulgaris	recent	0.05	0.000
Lolium perenne	recent	0.05	0.000
Medicago lupulina	recent	0.59	0.000
Medicago sativa	recent	0.13	0.014
Melampyrum arvense	recent	0.15	0.007
Melilotus officinalis	recent	0.29	0.001
Onobrychis viciifolia	recent	0.13	0.015
Ononis repens	recent	0.19	0.004
Origanum vulgare	recent	0.59	0.002
Poa pratensis agg.	recent	0.56	0.000
Potentilla reptans	recent	0.13	0.016
Salvia pratensis	recent	0.38	0.000
Senecio jacobaea	recent	0.13	0.022
Thymus pulegioides	recent	0.08	0.000
Trifolium campestre	recent	0.13	0.016
Trifolium medium	recent	0.14	0.019
Trifolium pratense	recent	0.48	0.006
Trisetum flavescens	recent	0.47	0.000
Veronica chamaedrys	recent	0.27	0.001
Vicia cracca	recent	0.31	0.000

Plant functional traits separating indicator species from the species pool and biotic environment at recent and ancient grasslands

We could identify several characteristics of indicator species that separated them from the residual species pool of the study area. Detailed test results for all traits are given in the appendix 8, while mean values or trait attribute distributions are depicted in figure 10 for all traits in which indicators differed significantly from the species pool.

Some traits and strategies seemed to be important for both, becoming an indicator of ancient and of recent grasslands. Other traits only mattered for one indicator species group.

Traits that separated both indicator species groups from the species pool were canopy height, Ellenberg indicator value for nitrogen and percentage affiliation to Grimes C- and S-strategy. The comparisons in figure 10 between mean values of the indicator species groups and community weighted means for the different grasslands show, that regarding all these characteristics, the indicators for ancient and recent sites diverged from the species pool values in opposite directions. Thus, while indicators of ancient sites tended to be extraordinary small, indicators of recent grasslands were among the tallest species of the species pool etc..

Traits only important for ancient grassland indicators were the Ellenberg indicator value for light and the minimum germination temperature, which were on average higher than of species in the species pool, and the seed production, which was on average lower than for species of the species pool.

Recent indicator species were further separated from the species pool by the proportion of hemerochorously dispersed species, by their leaf distribution (hardly any rosette) and by the average affiliation to Grime´s R-strategy, which was higher than at the residual species pool. Also the proportion of species with high lateral spread (>250 mm per year) and the proportion of legumes were especially high in the recent grassland indicator group. Recent grassland indicators further tended to have higher terminal velocities of seeds than species of the species pool.Community weighted means of almost all functional traits that separated indicators from the species pool differed significantly between the plots of ancient and recent grassland (means and results of Mann-Whitney U-tests are given in appendix 9). Only single trait attributes of nominal traits did not differ in percentage cover between ancient and recent grasslands: cover of semirosettes, cover of species with lateral spreads <100 mm/year and those with >250 mm/year.

Mean values from ancient grassland indicators over ancient and recent grassland plots to recent grassland indicators showed mostly a consistently rising or declining trend, such that

the trait values of the respective indicators tended to be below or above the mean community values even of their main habitat (figure 10 A-K).

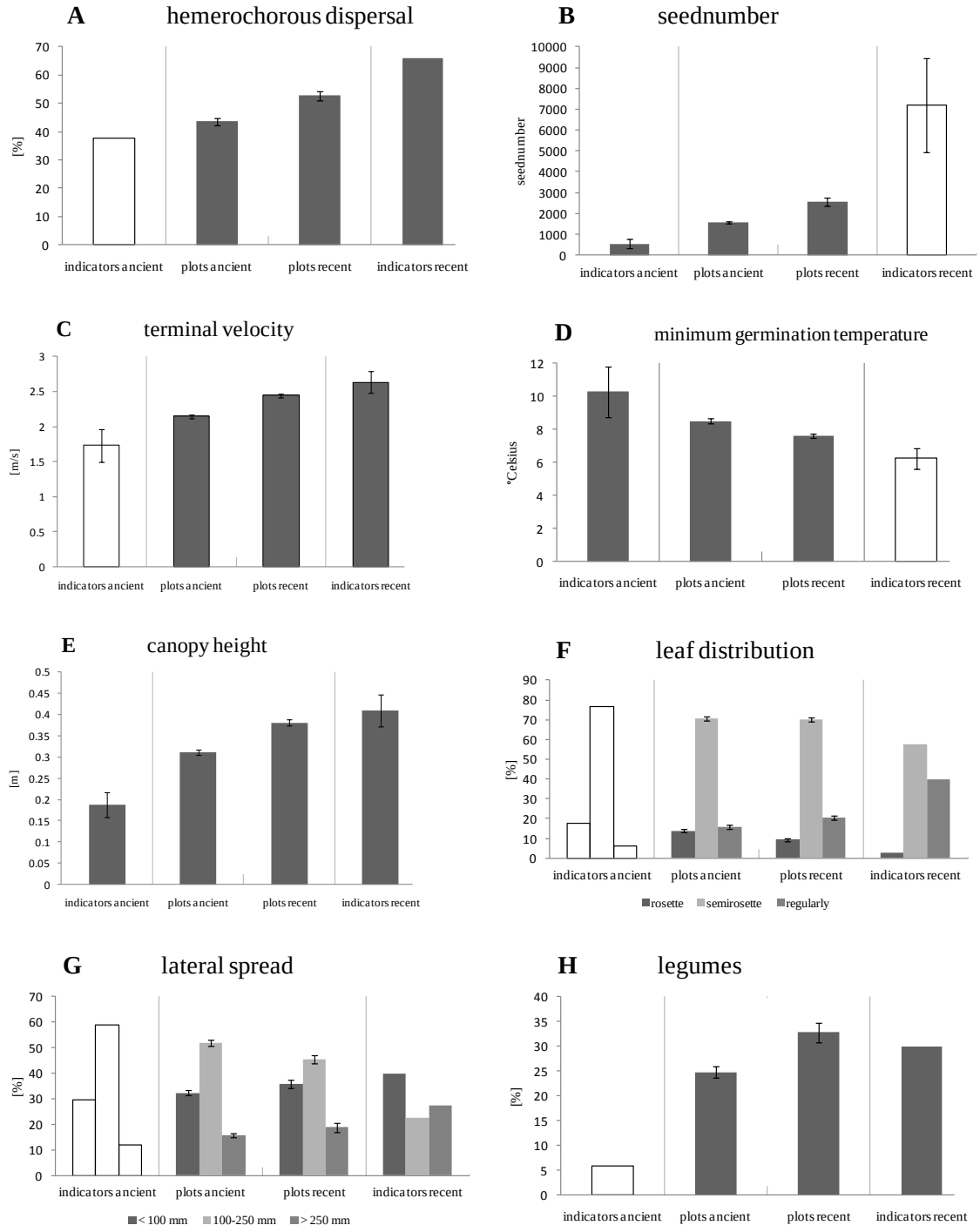

Figure 10: Comparison between mean trait values/attribute distributions of the indicator species of ancient and recent grasslands and the community weighted means of the traits/percentage cover of trait attributes for ancient and recent grassland plots (only for traits significantly differentiating indicators from the species pool, see appendix 8). White bars indicate that this trait only separated the coloured indicator species group from the residual species pool.

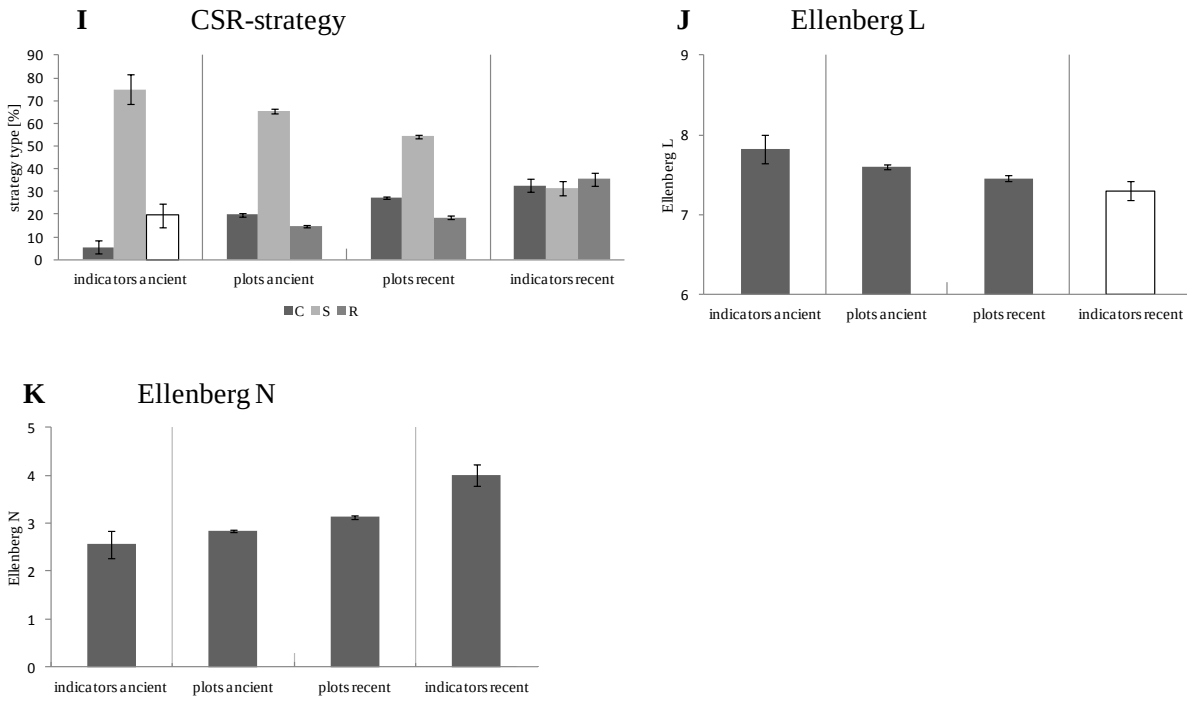

Figure 10: continued

Discussion

Importance of abiotic conditions for vegetation differences between ancient and recent grasslands

The axes separated the grasslands according to their age but did not show correlations with environmental factors like K- or P-content, water holding capacity, soil depth etc.. This implied that abiotic conditions could not explain differences in vegetation and thus indicator species occurrences. However, the mechanisms setting the relationship between nutrient capital and availability in the soil are still poorly understood (Gough & Marrs 1990) and important values describing nutrient availability might have been missed. It has been suggested that P:N ratio might be an important value (Fagan *et al.* 2008) and that as long as P is not the limiting factor, species of ancient grasslands could fail to establish on restoration sites.

Which species are indicators for ancient and recent grasslands?

We identified 17 indicator species for ancient grasslands and 40 species for recent grasslands. The classification of species into indicators for ancient and recent grasslands is highly stable over numerous studies and only singular species were grouped into the opposite indicator species group in other studies on calcareous grasslands (Gibson & Brown 1991; Lindborg &

Eriksson 2004; Fagan *et al.* 2008). Indicators of ancient calcareous grassland sites are often rare and threatened habitat specialists (late successional species), whereas recent grassland indicators were summarized as often weedy species associated with arable cultivation (early successional species) and also species typical for mesic grasslands (Hutchings & Booth 1996b; Kleijn 2003; Lindborg & Eriksson 2004).

Which traits or strategies separated indicators from the residual species pool of the study site?

The traits which separated the indicators from the residual species pool might be roughly grouped into traits that describe competitive ability of a plant (CSR-strategy, canopy height, vegetative lateral spread, leaf distribution, Ellenberg values for nitrogen and light), traits related to regeneration strategy (seed number per ramet , minimum germination temperature) and traits that describe the source of the species (terminal velocity, hemerochorous dispersal and therewith connected high legume proportion).

Only traits related to competitive strength of the species were as well important for ancient as for recent indicator species. Indicators of recent grasslands tended to be tall, mostly having semi-rosettes or regularly distributed leaves, comparatively high Ellenberg values for nitrogen and a high proportion of species had high lateral spread. This trait combination leading to competitive strength was further reflected by the high affiliation to Grimes C-strategy. High affiliation to Grimes C-strategy is typical for species which are tall, have a large peak biomass and which have the capability to spread by vegetative means and thus grow well in closed, productive grasslands (Grime 1979).

In the group of the indicators of ancient grasslands stress tolerators sensu Grime were over represented. Since in Grimes triangular ordination stress tolerance and competiveness are negatively correlated, high stress-tolerance values also imply poor competitive performance (Loehle 1988; Pywell *et al.* 2003). Poor competiveness of ancient grassland indicators was also given by low stature, high Ellenberg values for light and low values for nitrogen.

The separation between ancient grassland indicators being poor competitors versus recent grassland indicators being strong competitors was in accordance with other studies (Fagan *et al.* 2008).

Ancient grassland indicators had on average a higher germination temperature requirement than non-indicator species and produced significantly fewer seeds. It has been shown for forests that specialist species are sensitive to isolation due to a set of inter-correlated traits, including their low seed number (Hermy *et al.* 1999; Dupré & Ehrlen 2002). Hence, the low

seed numbers of indicator species for ancient grasslands may indicate that these species are stronger affected by isolation and have more difficulties to reach the recent grasslands.

The importance of germination related traits for species occurrence has been pointed out in numerous studies (Grubb 1977; Silvertown 1980b; Thompson *et al.* 1996). The need for higher temperatures for germination is a typical characteristic for late successional species of less fertile habitats and for species with gap dependend germination (Olff *et al.* 1994; Thompson *et al.* 1996), while early successional and ruderal species typical for arable fields tend to germinate at lower temperatures directly after seed fall, when the canopy is still open after previous management (Olff *et al.* 1994).

A significantly higher proportion of the recent grassland indicators was hemerochorously dispersed and N-fixating compared to the residual species pool. Many of the recent grassland indicators are known to have been cultivated, or introduced with former agricultural practice as weeds (Poschlod & WallisDeVries 2002). To the formerly cultivated species belong many legumes like *Onobrychis viciifolia, Medicago sativa, Melilotus officinalis* and *Trifolium pratense* (Königliches statistisch-topographisches Bureau 1870; Gradmann 1950; Lohmeyer & Sukopp 1992). Their N-fixation ability made them good fodder plants on poor soils. Among recent grassland indicators were further weedy species, which are associated with arable cultivation, like *Convolvulus arvensis, Cerastium arvense* or *Linaria vulgaris*.

Low values of terminal velocity indicate that seeds have good chances to be transported by wind due to being smaller, lighter or "wingier" (Kleyer *et al.* 2008). Thus, high terminal velocities of recent grassland indicator species may rule out long distance dispersal by wind as origin.

High rates of ruderality among the recent grassland indicator species indicate rapid germination and often short life cycles with heavy allocation to reproduction (Grime 1979). Hence, indicators of recent grasslands might have dominated seed bank and seed rain when cultivation ceased (Hutchings & Booth 1996a). Subsequently, recent grassland indicator species may have constituted the initial floristic composition and thus the the biotic environment right after abandonment of the sites. Apparently, they persisted on recent grasslands since the end of arable cultivation and impose a biotic filter for indicator species of ancient grasslands ever since.

Importance of biotic filter for indicator species occurrence

The pattern of consistently rising or declining mean values from ancient grassland indicators over ancient and recent plots to recent grassland indicators may imply that the restrictions of

ancient grassland indicator species to ancient grasslands may have been indeed due to biotic constraints.

Higher competitive environment at recent sites was indicated by slightly but significant higher canopy height, higher proportion of species with regularly distributed leaves, lower mean Ellenberg values for light and higher mean Ellenberg values for nitrogen, which were shown to be correlated with higher biomass production (Schaffers & Sýkora 2000).

Former investigations showed that also those small differences in plant statures may exercise critical effects on species survival and abundance (Givnish 1982).

The results showed that the recent plots were dominated by competitive species, while plots at ancient grasslands provided an environment to the ancient indicator species that was less competitive. Invasion resistance caused by particular resident species or functional groups has been found in previous studies. Freville (2007) showed that small species were only favored at low biomass plots and taller ones at high biomass plots. It has been also suggested by Kleijn (2003) that competitive processes determined failure of ancient grassland indicator species on former arable land dominated by large plants. Since first colonists on ex-arable fields are usually weedy species germinating from the seed bank, competition for light and other resources may become severe very rapidly after end of agricultural use (Pywell *et al.* 2003).

Along with differences in biotic environment between ancient and recent grasslands, changed abiotic conditions, like availability of photosynthetic active radiation and course of temperature at the ground etc., can be expected. It has been shown that light availability at the ground is crucial for germination and establishment of poor competitors (Hautier *et al.* 2009). Thus, biotic environment at recent sites may have been unsuitable as well for germination as for establishment of the small, ancient grassland indicators with gap dependent germination and high Ellenberg values for light.

For indicators of recent grasslands biotic filtering could not be an explanation for their restriction to recent sites, since invasion of a less competitive environment should not be an obstacle if abiotic conditions are the same. Nevertheless, abiotic conditions at the recent grasslands of our study have changed dramatically since the end of agricultural use and today soil fertility is comparable to ancient grassland sites (Karlik & Poschlod 2009). The low cover values of recent grassland indicators at ancient sites might show that these species reached the edge of their niches regarding soil fertility at the ancient grasslands, while they persisted on recent sites due to the inertia of the vegetation. Such high persistence of vegetation composition despite changes of environmental conditions is not uncommon (Egler 1952;

Ellenberg 1952; Pakeman *et al.* 2002). Impact of assembly history, means the sequence of species arrival at a site, and thus initial floristic composition has been studied extensively and given a prominent role for outcomes of community assembly in many cases (Robinson & Dickerson 1987; Drake 1991; Chase 2003; Ejrnaes *et al.* 2006; Petermann *et al.* 2010). The importance of initial floristic composition has been explicitly stressed for restoration success of former arable fields to calcareous grasslands (Fagan *et al.* 2008).

Conclusion

Although agricultural use dates back decades or even over a century, the indicator species of recent grassland were competitive species adapted to higher nutrient availability, first to flourish in secondary succession and often introduced to the former arable fields by humans as crop or as arable weed. This clearly stressed the importance of assembly history and thus of the initial floristic composition (Egler 1952) that developed after cessation of agricultural use for the actual species composition of the recent grasslands.

It has been shown that abiotic conditions at recent sites, like nutrient availability, were comparable to ancient sites and could not explain differences in vegetation composition between ancient and recent sites. Nevertheless, biotic environment of recent grasslands was still shaped by the traits of those more competitive species. Thus, the restriction of ancient grassland indicators to ancient sites was better explained by the more competitive biotic environment of recent sites, hampering regeneration and establishment of ancient grassland indicators, than by unsuitable environmental site conditions.

Therefore, the role of the biotic filter at grassland restoration should not be neglected. And once again the importance of remnant grasslands as refugia for threatened and rare grassland species has to be pointed out (Dzwonko & Loster 1998; Cousins & Lindborg 2008), as secondary grasslands may hardly fulfill those species' requirements on abiotic or at least, like in this study, biotic environment.

Chapter 7

Linking assembly rules with nature conservation and restoration practice

It has been claimed that the long-term viability and credibility of restoration practice needs an understanding of the basic ecological processes that operate at a site (Montalvo *et al.* 1997). Therefore, insights from basic community ecology must be adapted and translated into practical management (Palmer *et al.* 1997; Halle & Fattorini 2004; Young *et al.* 2005).

There is a mutual benefit of linking restoration but also conservation practice with other biological disciplines. Restoration and conservation projects offer the settings in which to test and develop ecological theories. In turn, ecological theories and unraveled mechanisms of community assembly can increase the understanding of ecological processes and thus can improve the tools of restoration and conservation ecology (Lake *et al.* 2007).

Amongst others, those mutual benefits have been demonstrated for the linkage of restoration practice with landscape ecology. It has been proven that the benefits of utilizing restoration efforts to test landscape principles are relatively straightforward (Bell *et al.* 1997). In turn, restoration efforts can profit from landscape concepts as they can provide suggestions for appropriate spatial configurations of restored elements to facilitate recruitment of flora and fauna (examples given in Bell *et al.* 1997).

Likewise, awareness of the importance of other biological disciplines for restoration and conservation practice has arisen. Especially the field of conservation genetics can provide valuable knowledge for restoration of self-sustaining populations or for defining which populations are of highest conservation value. Studies on genetic variation within and between populations or on geneflow can help to elaborate management implications (Montalvo *et al.* 1997; McKay *et al.* 2005). A further topic with relevance for restoration and conservation practice is the choice of source material for species introductions. In respect thereof, genetic studies can elucidate the importance of taking local ecotypes and help to define those (Hufford & Mazer 2003; Smith *et al.* 2005; Bischoff *et al.* 2010).

As demonstrated in the present thesis and exposed in the following, also the analysis of plant trait based rules and mechanisms of community assembly can provide valuable information

not only for the field of basic community research but also for the conservation and restoration of grassland plant communities.

Effects of grassland management regimes on species assembly processes and implications for nature conservation and restoration

Three chapters (chapters 2, 3 and 4) of this thesis dealt with the effects of different grassland management treatments on plant assembly processes. Therewith, they gave attention to a current problem of nature conservation. Species-rich, extensively used grasslands are of major conservation value. Their typical species composition developed under grazing. For centuries grazing was at most compensated by mowing for hay-making purpose (Poschlod & WallisDeVries 2002). However, today these traditional treatments are difficult to continue due to economic and organizational reasons at many sites. Now, it is the task of nature conservation to define suitable alternative management treatments.

It has been shown that it is not always necessary to re-establish or continue the natural or historic disturbance regimes, but that periodic disturbances mimicking former disturbance events may also succeed to conserve or restore former species composition (Friedman *et al.* 1995; Palmer *et al.* 1997). Thus, it has to be asked for each ecosystem: what is the minimum level of manipulation required to mimic natural or historic disturbance (Briemle *et al.* 1991)?

In case of the studied formerly grazed grasslands it has to be stated that the conservation of their typical species composition may not be possible at low costs. All management treatments not applied each year, no matter if it was burning, mulching or abandonment, clearly failed to conserve the species composition of formerly grazed sites: either due to increasing competition eliminating poor competitors (chapter 2,3), management specific trait selection pressures (chapter 3) or due to reduced possibilities for generative regeneration (chapter 4). However, also once per year applied management treatments like mulching or burning failed in this regard. Only mowing once per year – one of the traditional management treatments of ancient grasslands besides grazing – succeeded to maintain the functional group composition of the grazing treatment. However, trait selection pressures and chances of generative recruitment could not be tested for mowing once per year in this thesis – thus no final conclusions on these aspects can be given.

Mulching twice per year also has not been tested for germination niches and chances of seedling survival. Nevertheless, the results of the plant functional group composition showed only a very slight increase of the competitive species group at the study site, which did not lead to a decline of other functional groups (chapter 2) and the trait selection pressure over

several grassland sites was very low at this treatment (chapter 3). Thus, mulching twice per year may also be regarded as suitable alternative management treatment to maintain functional and floristic diversity of formerly grazed grasslands. Other treatments may succeed to keep the landscape open but may fail to maintain the species composition of formerly grazed (or mown) ancient grasslands.

Hence, the current thesis demonstrated that the replacement of grazing by alternative management treatments should be well-considered. Thus, instead of searching for grazing substitutes, it may be a more promising approach to elaborate cost-effective grazing management regimes which combine the positive effects of grazing on species composition with economic requirements. Many research projects have been set up for this purpose in the last years (Härdtle *et al.* 2002). Those projects which focus on prospects and perspectives of semi-open pasture landscapes, with grazers remaining year-round in fenced zones with minimal supervision in a "semi-wild" state, could become a promissing conservation concept (Härdtle *et al.* 2002; Bunzel-Drüke *et al.* 2008).

Small scale assembly processes, biodiversity effects and their implications for nature conservation and restoration

The study of species diversity, particularly the creation and maintainance of local and regional diversity, is central to community ecology (Palmer *et al.* 1997). Accordingly, the conservation and restoration of biodiversity is the aim of many efforts in nature conservation and restoration. Therefore, knowledge on the creation of biodiversity and its importance for ecosystem processes is of interest for theory and practice.

But also if restoration ecologists do not focus on the maximization of species number but on the management of endangered species, it is important to understand how biodiversity influences the establishment and persistence of focal species (Palmer *et al.* 1997).

Our study on establishment success of typical grassland species dependent on small scale environmental differences in a calcareous grassland pasture (chapter 6) showed that establishment chances were best at plots with high diversity on small scale. Therewith, small scale diversity seemed to be a result of the community being highly invasible.

The results indicated that these higher invasible plots offered a less competitive environment. Hence, what has been found for the comparison of management treatments based on functional group composition (chapter 2) and on species selection pressures (chapter 3) hold true for the analysis on smallest scale: in the studied grasslands highest invasibility and

therewith diversity (species and functional trait diversity) can only be reached when competition is low.

The often claimed higher invasion resistance of more diverse communities, supporting importance of sampling effects or more complete resource use at higher diversity, did not apply to the calcareous pasture of our study. Therewith, generative regeneration and persistence of endangered typical calcareous grassland species should be enhanced the higher the small scale species diversity of the particular site is.

Furthermore, the analysis on small scale assembly processes (chapter 6) gave hints for facilitation playing a role as the hemiparasitic species *Rhinanthus minor* tended to be more succesfull in plots with higher cover values of host species. A sown legume (*Anthyllis vulneraria*) tended to be less successful in plots with higher cover values of other legumes. Those mechanisms have to be validated in more comprehensive experiments. If these mechanisms turn out to effect establishment success of target species in more specific experiments the results may also be incorporated in restoration practice.

Implications for the restoration of calcareous grasslands on former arable fields

It is the aim of nature restoration projects not only to restore abiotic conditions but whole plant (and animal) communities. As the hypothesis "if you built it (the habitat) they will come", has already been dispelled as a myth (Hilderbrand *et al.* 2005; Poschlod & Biewer 2005), restoration ecology is forced to work on an understanding of the functioning and assembly of natural communities (Renker *et al.* 2004).

Several studies focused on opportunities and limitations of restoration of former arable fields to valuable grasslands (Willems 2001; Pywell *et al.* 2002; Kleijn 2003; Pywell *et al.* 2003; Lawson *et al.* 2004; Kiehl & Wagner 2006; Karlík & Poschlod 2009), often pointing to the importance of seed availability of target species or soil conditions as crucial factors for restoration success.

The current study on always grazed ancient grasslands and recent grasslands on former arable fields (chapter 6) pointed to further restoration success limiting factors. We demonstrated that site history can be the decisive factor for restoration success due to biotic filtering caused by the initial floristic composition.

Therefore, considering the biotic environment in terms of functional traits of the different sites together with the traits of indicator species can help to explain limited restoration success

of former arable sites. For restoration of grasslands on ex-arable fields biotic environment created by the initial floristic composition and biotic filtering mechanisms should be given particular attention for predictions on restoration prospects.

The previous section aimed to define which management regimes are suitable for the conservation of ancient grasslands. Grazing and most likely also mowing and mulching twice per year proved to be appropriate to maintain species and functional trait richness of ancient grasslands (chapter 2, 3, 4). However, as shown in chapter 6 for the restoration of former arable fields (or otherwise degraded grasslands) even those management treatments can fail to bring back the former species composition and especially indicator species of ancient sites. Dependent on the specific site this failure may not only be due to seed limitation or inappropriate soil conditions but also due to the high inertia of vegetation once competitive species took over and thus due to biotic filtering.

Value of long-term experminents for basic and applied ecology

As has been shown in the study on functional group development at different management treatments (chapter 2), mechanisms behind species changes became visible only after decades. That new equilibria of functional group composition were not reached after almost 30 years backed up the necessarity to keep up those long term experiments. Furthermore, the results indicated that conclusions on effects of environmental change on vegetation should not be set up premature. At least in the case of the studied grasslands, inertia of the vegetation was very high (chapter 2 and 6). For the fallow experiments predictions made after six years on the suitability of management treatments to maintain the original species composition of grazed sites (Schiefer 1981, 1983) did not match the results of our analysis indicating that hardly any alternative management treatment would conserve species and functional composition of the traditional grazing treatment (chapter 2 and 3).

The results of the current thesis demonstrated that data collected from restoration or conservation projects, like the 30+ year covering data of the “fallow experiments”, can enhance research and application of conservation and restoration ecology as well as basic ecological theory. The gained insights based on long-term experiments underline that the value of those experiments for a multitude of biological disciplines can hardly be overrated (Silvertown *et al.* 2006; Schreiber *et al.* 2009).

Conclusion

A mutualistic relationship between research on assembly rules and conservation and restoration practice clearly exists. For all our analyses we used data from study sites incorporated in nature conservation projects running for decades. Without those projects the database for assembly rule research would have been missing and mechanisms of species assembly like found in our studies would not have been detectable due to the high inertia of vegetation. Only the long run-time of conservation projects (and data collected from their beginning) allowed insights into assembly processes.

Thus, it should be highly recommended to utilize the potential of conservation and restoration projects by regular data collections (on vegetation, fauna, soil etc.) from the start. Therewith, conservation and restoration projects can provide a basis for the development of ecological theories and for an understanding of processes underlying vegetation changes.

Likewise, it could be demonstrated that research on functional traits and assembly rules can give valuable insights and indications for restoration and conservation practice that may be further elaborated.

Perspectives

Based on the current thesis, proposals for future research may be set up. Those concern on the one hand proposals advancing the field of assembly rules research by further validation of found mechanisms and test of their transferability to other sites and ecosystems. On the other hand, the benefits from linking biological disciplines should be worked out.

- Available data on long-term restoration and conservation projects should be used for analyses on functional mechanisms driving vegetation development to finally improve actions within restoration and conservation ecology.
- Mechanisms of species assembly processes found in this thesis should be validated with experiments designed more specifically to test single assumptions. This may be reasonable for the mechanisms that were suggested to play a role for small-scale assembly processes in chapter 6.
- Mechanisms behind vegetation development should be analysed for various ecosystem types to test their transferability and to answer the question which ecological theories apply to which ecological system.
- Further improvements in the field of restoration and conservation ecology should be possible through a stronger linkage with knowledge from other ecological disciplines,

like it has been shown for the connection with research on (trait-based) assembly rules in this thesis.

- Not only exclusive linkage of other biological disciplines with nature restoration and conservation promises mutual benefits. Also the linking of (trait-based) assembly rule research with other ecological disciplines, like population genetics, could broaden our understanding of the mechanisms causing vegetation changes.

Summary

Consecutive filtering processes cause that local plant communities are composed by subsets of species available in the regional species pools. Those filters act at increasingly finer spatial scales on the species belonging to the species pool. Only plants that are able to reach the site and which can pass the climatic and edaphic filter, can be filtered out by the disturbance regime and finally by biotic interactions.

As plants are adapted to their environment by their traits, plant traits are the filtering units of these processes involved in plant community assembly. Plant traits that make the plant fit into or respond to a certain environment are defined as functional. It has become a prominent approach in community ecology to search for assembly rules implied by the different filters based on plant functional traits.

The current study put into focus assembly rules in grassland communities in southwest Germany. These grasslands were created by livestock grazing or mowing at least since the Roman period and constitute habitats for a multitude of rare and threatened species. Furthermore, especially calcareous grasslands stand out by extraordinary high small scale species richness. Unfortunately, the traditional use of those grasslands became more and more unprofitable in the course of industrialization during the 20th century. Large parts of the formerly connected open farming landscape with extensively used grasslands were transformed by fertilization, drainages and/or liming but also abandonment to less valuable habitats from a conservation point of view. Thus, remaining extensively used grasslands are of high conservation value today. As semi-natural habitats they depend on some form of management to maintain their typical species compositions. It is the task of conservation biologists to determine appropriate, alternative management treatments to the original grazing treatment which can hardly be continued due to economic and organizational reasons on many sites.

Another challenge has become the restoration of valuable grasslands on former arable fields that were abandoned due to agricultural intensification. Even after decades and with ancient grasslands close by and original management practices reintroduced those restored grasslands consistently fail to resemble the typical plant composition of the original grassland types of the restoration sites.

Facing problems to maintain and restore valuable plant communities, an understanding of the mechanisms and rules driving species assembly has become even more urgently needed. The

current thesis intended to link basic assembly rule research with questions concerning grassland conservation and restoration.

In chapter 2 we determined plant functional groups that are important with regard to land use types (grazing, mowing, mulching, burning, abandonment) and looked for mechanisms leading to changes in species composition after management changes in calcareous grasslands.
To filter out the set of traits which best described the variation in plant composition along the studied land use gradient and to identify functional groups we chose an iterative three-table ordination method. We included traits related to persistence as well as traits describing the germination niche of a plant. To gain insight into underlying mechanisms which led to differing importance of these plant functional groups at different management regimes we investigated shifts in dominance of the identified functional groups at eight management regimes using long-term vegetation data of a site which was grazed before the onset of different management regimes in 1974. Ongoing unidirectional changes in cover of the four determined functional groups at most of the treatments indicated that even after almost 30 years new equilibria of functional group composition were still not reached.
The study showed that other management treatments but grazing and mowing led to changes in functional group composition, which were mainly driven by increasing dominance of a highly competitive species group.

In chapter 3 we focused on plant extinctions and invasions in differently managed grasslands over the time span of more than 30 years. First, we asked if different management treatments (grazing, mulching twice per year, mulching once per year, burning once per year, abandonment) differed with regard to invasibility or plant extinction numbers. Secondly, we performed a pooled analyses and a meta-analysis over six sites per management treatment contrasting invaders and extinct species traits to find management dependent effects of trait selections.
The different management treatments did not differ in invasion rates. This could originate either from seed limitation, from very low establishment success at all management treatments or a combination of both factors. In contrast, extinction rates differed significantly between the treatments. Extinction rates increased from grazing, mulching twice, mulching once and burning to abandonment. The mean number of invasions exceeded the number of extinctions only at grazing, while that relation was reversed at the other management treatments.

Accordingly, the trait based analyses showed that least trait selection occurred at the grazing treatments and at mulching twice per year, while strongest trait selection pressures acted at abandonment. Management specific trait selection patterns could be revealed, e.g. the selection for higher seed masses reached the highest effect size at mulching once per year - most probably due to the dense litter layer – while burning favoured the invasion of species with lower Ellenberg values for moisture and nutrients. Furthermore, the meta-analysis indicated that at all management treatments invaders tended to be more competitive than extinct species.
Only at grazing and mulching twice per year trait selection pressures were low what resulted in low species extinction numbers. At these two managements extinct and invading species were almost a random draw from the species pools. Therewith only these two managements should allow to maintain not only high species diversity but also high functional diversity on the long run.

Chapter 4 presented the results of a sowing experiment with 15 typical grassland species at four different management treatments (grazing, burning once per year, mulching once per year and abandonment). This experiment should help to evaluate the relative roles of seed and germination niche limitation as well as seedling survival at the different management treatments of calcareous grassland. In half of the plots per grassland management treatment litter and bryophyte cover were removed prior to sowing to simulate disturbance.
At most of the species germination rate was only significantly affected by the removal of litter and bryophyte cover and not by the management treatments. Seedling survival rate, however, was affected by the management treatment becoming the driving force for successful establishment.
The availability of germination niches plus the survival chances under different management regimes both influenced population development at differently managed grassland. The degree of seed limitation was low at all management treatments. Nevertheless, judging over abandonment, burning, mulching and grazing our results indicated, that the grazing treatment should offer best conditions for successful regeneration by seeds.

In chapter 5 we searched for mechanisms of biotic filtering in the invasion process of the 15 sown species at the grazing treatment which proved to offer best conditions for germination and establishment as shown in the previous chapter. Germination of all species was artificially enhanced by moss and litter removal to get enough seedlings to be able to detect patterns of neighbourhood filtering influencing seedling survival and final establishment after three

growing seasons. Several neighbourhood characteristics were recorded, like neighbour species identity and neighbour species traits in 10 cm radius around the seedlings, vegetation cover and height in spring and summer, bare ground, litter layer etc..
Next, plots with successful survival of the sown species until the last census were contrasted against plots that did not permit survival.
Establishment of all species was generally very poor and only individuals of eight species survived until the final census. Despite many seedlings and juveniles may have died due to unforeseeable events, some patterns of possible neighbourhood filtering mechanisms emerged.
We found hints for facilitation playing a role, e.g. host species occurrence could have influenced *Rhinanthus minor* establishment. *Anthyllis vulneraria* tended to be more successful in plots with less cover of other legumes.
Species diversity turned out to be most significant in our analysis. The survival of all species tended to be higher in plots with higher species richness. On one hand, this could also point to importance of facilitative effects as higher species richness might raise the chance of a species being present which facilitates invasion. On the other hand, higher species richness was correlated with a number of other plot characteristics mainly pointing to a less competitive environment at high diversity plots.
Therewith, our study pointed out that also in natural systems mechanisms of biotic filtering through neighbouring plants may control small scale species assembly.

Finally, we wanted to elucidate possible reasons for the frequent failure of grassland restorations on former arable fields with a trait based approach in chapter 6. Therefore, we extracted indicator species of adjacent ancient and recent grasslands with comparable abiotic conditions and analysed reasons for the restricted occurrence of indicator species. We asked which functional traits make the indicator species stand out from the species pool and also questioned the role of biotic filtering for species failure in the other grassland type.
Indicator species of recent grasslands were competitive species adapted to higher nutrient availability and often introduced to the former arable fields by humans as crop or arable weed. Hence, they might have persisted at recent sites since the end of agricultural use despite changes in abiotic conditions.
Indicators of ancient grasslands were small species with specific requirements for germination and establishment. Comparisons of community weighted means for functional traits that separated the indicators from the species pool showed significant differences between ancient

and recent grasslands. Our results suggested that indicators of ancient sites might have failed at recent sites due to higher competitive environment and thus biotic filtering.

Chapter 7 gives conclusions and perspectives focusing on the use of the current findings for restoration and conservation practice. It has been claimed that an understanding of processes operating at a site is crucial for advancements in restoration and conservation practice.
As the results of the single chapters elucidated which mechanisms drove plant species assembly dependent on management regime or site history, they were well suited to be reconsidered with respect to their value for grassland restoration and conservation. Especially the mutual use of assembly rule research and conservation practice had to be stressed. While conservation and restoration projects offer the settings to test and develop ecological theories, they can in turn benefit from understanding how plant communities assemble.
It should be aimed at a stronger linking of biological disciplines and therewith a translation of findings of other biological disciplines, like assembly rule research, into restoration and conservation practice. Future research would be needed to test the transferability of our results to other sites and ecosystems and to validate the importance of the assumed mechanisms.

Zusammenfassung

Lokale Artengemeinschaften setzen sich immer nur aus einem Teil der Arten des regionalen Artenpools zusammen. Damit Arten des regionalen Artenpools in einer lokalen Artengemeinschaft vorkommen können, müssen sie mehrere Filter erfolgreich durchlaufen haben. Diese aufeinander folgenden Filter agieren auf zunehmend räumlich begrenzten Ebenen. Zunächst müssen die Arten auf eine Fläche gelangen können, dann den klimatischen und den edaphischen Filter passieren, danach an das jeweilige Störungsregime angepasst sein und schließlich können biotische Interaktionen mit der unmittelbaren Umgebung über das Vorkommen einer Art entscheiden.

Arten sind anhand ihrer Merkmale an ihren Lebensraum angepasst. Daher sind die Merkmale der Pflanzen die Einheiten, nach denen die einzelnen Filter Arten aussortieren. Merkmale, deren Besitz dazu führt, dass eine Art in eine Gesellschaft „passt“, oder aufgrund derer eine Art auf Umweltänderungen reagiert, sind als funktionelle Merkmale definiert. Mittlerweile ist es in der Synökologie eine beliebte Herangehensweise Regeln zu erarbeiten („assembly rules“), nach denen die verschiedenen Filter Arten aufgrund ihrer Merkmale aussortieren.

Die vorliegende Arbeit beschäftigte sich mit Regeln, die zur jeweiligen Artenzusammensetzung von Grünland führen. Hierfür wurden Grünlandflächen in SW-Deutschland untersucht, welche seit der Römerzeit durch Beweidung und Mahd entstanden sind. Extensiv genutztes Grünland bietet einer Vielzahl seltener und bedrohter Pflanzenarten einen Lebensraum. Kalkmagerrasen zeichnen sich in besonderem Maß durch außerordentlich hohe Artenzahlen auf kleinem Raum aus. Leider wurde die traditionelle Nutzung von Grünland durch die Industrialisierung während des 20. Jahrhunderts zunehmend unrentabel. Dies führte dazu, dass große Teile der ehemaligen Kulturlandschaft mit ihren weitläufigen Grünlandflächen durch Düngung, Drainagen und/oder Kalkung, aber auch durch ausbleibende Nutzung in naturschutzfachlich wertlosere Flächen überführt wurden. Daher sind heute noch existierende, extensiv genutzte Grünlandflächen von besonderem Interesse für den Naturschutz. Als halbnatürlicher Lebensraum ist Grünland von kontinuierlicher Pflege abhängig, um die typische Artenzusammnensetzung aufrecht zu erhalten. Aktuell ist es die Aufgabe des Naturschutzes, geeignete alternative Pflegemaßnahmen zur ursprünglichen Beweidung oder Mahd festzulegen, da gerade die Beweidung sowohl aus wirtschaftlichen als auch aus organisatorischen Gründen auf vielen Flächen nicht mehr durchführbar ist.

Eine weitere Herausforderung stellt die Restitution von Grünland auf Ackerbrachen dar, welche im Zuge der Intensivierung der Landwirtschaft aus der Nutzung genommen wurden. Bei Grünland, welches auf Ackerbrachen entstand, zeigte sich immer wieder die Problematik, dass auch nach Jahrzehnten die Artenzusammensetzung nicht an die Artenzusammensetzung kontinuierlich als Grünland genutzter Flächen heranreichte; selbst wenn solche alten Grünlandflächen sich in unmittelbarer Nachbarschaft befanden und die traditionelle Nutzung wieder eingeführt wurde.

Angesichts der Aufgabe wertvolle Artengemeinschaften zu erhalten bzw. wiederherzustellen, gewinnt das Verständnis von Mechanismen und Regeln, nach denen sich Artengemeinschaften zusammenfinden und verändern, zunehmend an Bedeutung. In der vorliegenden Arbeit wurden grundlegende Fragen zu den Regeln der Zusammensetzung von Grünland-Pflanzengemeinschaften mit Fragen betreffend dem Schutz und der Restitution von Grünland verknüpft.

Im 2. Kapitel bestimmten wir funktionelle Pflanzengruppen, welche auf den Faktor Landnutzung reagierten (Beweidung, Mahd, Mulchen, Brand, Brache) und untersuchten die Mechanismen, welche zu Veränderungen in der Artenzusammensetzung von Kalkmagerrasen nach Managementänderungen führten.
Um die Merkmale und schließlich die funktionellen Pflanzengruppen zu finden, welche am besten die Variation in der Artenzusammensetzung entlang des Nutzungsgradienten erfassten, wählten wir eine iterative Ordinationsmethode, welche auf drei Tabellen basiert (eine Vegetationstabelle, eine Tabelle mit Umweltvariablen und eine Tabelle mit Artenmerkmalen). Bei den Merkmalen wurden sowohl Merkmale, welche für die Persistenz von Arten bedeutend sind, als auch Merkmale, die die Keimungsnischen der Arten bestimmen, einbezogen. Um herauszufinden, welche Mechanismen zur unterschiedlichen Bedeutung dieser funktionellen Gruppen bei den verschiedenen Managementvarianten geführt haben, wurde die Entwicklung der Dominanz der einzelnen funktionellen Gruppen bei alternativen Pflegemaßnahmen ausgehend von traditionellem Beweidungsmanagement über einen Zeitraum von 30 Jahren untersucht. Die vier funktionellen Gruppen zeigten dabei häufig eine lineare Zu- bzw. Abnahme über die Zeit. Damit deutete sich an, dass sich bei fast allen alternativen Pflegemaßnahmen auch nach 30 Jahren kein neues Gleichgewicht hinsichtlich der Zusammensetzung funktioneller Gruppen eingestellt hatte. Nur bei Beweidung und Mahd blieb der Deckungsanteil der funktionellen Gruppen über die Zeit konstant. Bei allen anderen Pflegemaßnahmen fanden hingegen Verschiebungen der Deckungen funktioneller Gruppen

statt, welche hauptsächlich durch die zunehmende Dominanz einer besonders konkurrenzstarken Gruppe angetrieben zu sein schienen.

Im 3. Kapitel wurde ebenfalls die Entwicklung der Artenzusammensetzung auf Versuchsflächen betrachtet, welche seit 30 Jahren unterschiedlichen Pflegemaßnahmen unterworfen waren. Der Fokus wurde in dieser Studie auf Arten gelegt, die seit Einsetzung der Pflegemaßnahmen auf den Parzellen verloren gegangen bzw. eingewandert sind. Zunächst sollte die Frage beantwortet werden, ob verschiedene Managementvarianten (Beweidung, Mulchen, Brennen, Brache) sich hinsichtlich Invasibilität oder Anzahl aussortierter Arten unterscheiden. Zudem wurden sowohl eine zusammenfassende Auswertung über alle sechs Flächen als auch eine Metastudie durchgeführt, wobei jeweils für jedes Management Merkmale der eingewanderten Arten denen der verloren gegangen Arten gegenübergestellt wurden, um letztendlich managementspezifische Merkmalsselektionen aufzudecken.
Die Einwanderungsraten unterschieden sich bei den verschiedenen Pflegemaßnahmen nicht. Dieses Ergebnis könnte auf Samenlimitierung, geringen Etablierungserfolg bei allen Managementmaßnahmen oder auch auf eine Kombination beider Faktoren zurückzuführen sein. Im Gegensatz dazu unterschieden sich die Extinktionsraten signifikant zwischen den verschiedenen Managementvarianten. Diese nahmen von Beweidung über Mulchen 2x jährlich, Mulchen 1x jährlich, Brennen 1x jährlich und Brache zu. Nur bei Beweidung war die Anzahl der neuetablierten Arten im Mittel höher als die Anzahl lokal ausgestorbener Arten.
Dementsprechend zeigten die Auswertungen zu den Merkmalen ausgestorbener versus eingewanderter Arten, dass bei Beweidung und Mulchen 2x jährlich die geringste Selektion für oder gegen bestimmte Merkmalsausprägungen stattfand. Die stärkste Selektion fand hingegen bei den Bracheparzellen statt. Zum einen wurden mangementspezifische Merkmalsselektionen deutlich. So wurden z.B. bei Mulchen 1x jährlich besonders großsamige Arten bevorzugt – vermutlich aufgrund der massiven Streuschicht –, während bei Brennen Arten mit niedrigen Ellenberg Zeigerwerten für Feuchtigkeit und Nährstoffe gefördert wurden. Desweiteren zeigte die Metastudie, dass über alle Managementvarianten hinweg einwandernde Arten tendenziell konkurrenzstärker waren, als die, die verloren gingen.
Nur bei Beweidung und Mulchen 2x jährlich war der Selektionsdruck für bestimmte Merkmalsausprägungen gering. Dies spiegelte sich in einer geringen Anzahl verloren gegangener Arten und in der zufälligen Verteilung einwandernder und ausselektierter Arten über den Artenpool wider. Daher sollten bei Beweidung und Mulchen 2xjährlich auch

langfristig sowohl eine hohe Artenvielfalt als auch eine hohe funktionelle Diversität erhalten bleiben.

Im 4. Kapitel wurden die Ergebnisse eines Aussaatexperiments vorgestellt, bei welchen 15 typische Grünlandarten auf vier Parzellen mit unterschiedlichem Management (Beweidung, Brennen 1x jährlich, Mulchen 1x jährlich und Brache) ausgesät wurden. Dieses Experiment sollte dazu beitragen, die Bedeutung von Samenlimitierung, Keimungsnischenlimitierung und Überlebenschancen der Keimlinge abhängig vom jeweiligen Management zu bestimmen. Bei der Hälfte der eingesäten Plots je Management wurden die Moos- und Streuschicht vor der Aussaat entfernt und somit eine Störung simuliert und Keimungsnischen geschaffen.
Im ersten Jahr nach der Aussaat hatte diese künstliche Störung eine positive Auswirkung auf die Keimung fast aller Arten bei allen Managementvarianten. Letztendlich zeigte sich jedoch im dritten Jahr nach der Aussaat, dass das jeweilige Management sich entscheidend auf das Überleben der Jungpflanzen auswirkte und somit die treibende Kraft für deren Etablierungserfolg wurde. Sowohl die Verfügbarkeit von Keimungsnischen als auch die Überlebenschancen bei den verschiedenen Mangagementvarianten beeinflussten die Entwicklung der Populationen der ausgesäten Arten bei den verschiedenen Managementvarianten. Abschließend ließ sich feststellen, dass Samenlimitierung bei allen Managementvarianten nur eine geringe Rolle spielte, jedoch im Vergleich Beweidung die besten Voraussetzungen für die generative Regeneration der ausgesäten Arten bot.

Die Rolle des biotischen Filters für den Etablierungserfolg von 15 ausgesäten Grünlandarten auf der beweideten Parzelle untersuchten wir im 5. Kapitel. Die Beweidung eignet sich, wie im vorherigen Kapitel dargestellt, im Vergleich zu anderen Managementvarianten am besten für die generative Regeneration. Die Keimung der ausgesäten Arten wurde durch die Entfernung der Moos- und Streuschicht vor der Aussaat künstlich gefördert, um ausreichend Keimlinge zu erhalten, anhand derer sich die Auswirkungen der Nachbarpflanzen auf den Etablierungserfolg untersuchen ließen. Hierzu wurde eine Vielzahl von Faktoren aufgenommen, welche die von den Nachbararten geschaffene Umgebung beschrieben: die Identität der unmittelbaren Nachbararten und ihre Merkmale (im 10 cm Radius um die Keimlinge), Gesamtdeckung der Vegetation, Vegetationshöhe im Frühjahr und Sommer, Offenbodenanteil, Streuschicht etc..
Plots mit lebenden Individuen beim letzten Zensus wurden mit den Plots verglichen, bei denen alle Keimlinge/Jungpflanzen während des Untersuchungszeitraums abgestorben waren.

Insgesamt war der Etablierungserfolg aller Arten sehr gering und nur von acht Arten überlebten Individuen bis zum letzten Aufnahmezeitpunkt. Obwohl eine Vielzahl der Keimlinge vermutlich aufgrund unvorhersehbarer Ereignisse abgestorben sein dürfte, zeigten sich Muster, welche auf Auswirkungen der Nachbararten auf das Überleben hindeuteten.
Wir fanden Hinweise darauf, dass umgebende Arten das Überleben gefördert haben könnten. So kamen Wirte von *Rhinanthus minor* häufiger in Plots mit erfolgreicher Etablierung vor. *Anthyllis vulneraria* war hingegen erfolgreicher in Plots mit geringerer Deckung anderer Leguminosen.
Die Artenvielfalt der unmittelbaren Nachbarschaft zeigte sich als bedeutendster mit dem Etablierungserfolg zusammenhängender Faktor. Einerseits könnte dies darauf hinweisen, dass eine höhere Artenvielfalt die Chancen erhöht, dass eine Art dabei ist, die die Etablierung fördert. Andererseits war die Artenvielzahl mit einer Reihe anderer Plotcharakteristika korreliert, welche im Wesentlichen auf eine kleinflächig konkurrenzärmere Umwelt bei höherer Artenvielfalt hinwiesen.
Mit dieser Studie konnte gezeigt werden, dass sogar in natürlichen Systemen der durch benachbarte Arten geschaffene biotische Filter Auswirkungen auf kleinräumige Prozesse der Artenzusammensetzung haben könnte.

Im 6. Kapitel wollten wir schließlich mittels eines funktionellen Ansatzes mögliche Gründe für die so häufig scheiternde Restitution von Grünland auf ehemaligen Äckern aufzeigen. Hierfür wurden Indikatorarten von Grünland auf ehemaligen Äckern und Indikatorarten benachbarter, seit jeher beweideter, typischer Grünlandflächen bestimmt. Unterschiede in der Abiotik hinsichtlich Nährstoffversorgung bestanden zwischen den unterschiedlich alten Grünlandtypen nicht mehr. Wir untersuchten, welche funktionellen Merkmalsausprägungen die Indikatorarten aus dem Artenpool herausstechen ließen und hinterfragten ebenso die mögliche Rolle des biotischen Filters für den mangelnden Erfolg der Indikatorarten alter versus junger Weiden auf den jeweils anderen Grünlandtyp.
Indikatorarten des Grünlands auf ehemaligen Äckern waren konkurrenzstarke Arten, die an höhere Nährstoffzufuhren angepasst sind und oftmals mit der früheren Nutzung als Ackerunkraut oder Nutzpflanze eingeführt wurden. Von daher lag die Vermutung nahe, dass diese Arten trotz der Änderungen der abiotischen Bedingungen auf den Flächen seit der Nutzungsaufgabe der Äcker ausharrten.
Indikatorarten von altem Grünland waren hingegen kleine Arten mit besonderen Ansprüchen an die Keimung und an die Etablierung.

Vergleiche der gewichteten Mittelwerte funktioneller Merkmale für die beiden Grünlandtypen zeigten signifikante Unterschiede zwischen altem und neuem Grünland hinsichtlich der Merkmale, die die Indikatorarten von dem restlichen Artenpool abgrenzten. Die Ergebnisse legten den Schluss nahe, dass die Indikatorarten von altem Grünland auf den neuen Flächen aufgrund der von den dort vorhandenen Arten geschaffenen konkurrenzstärkeren Umgebung und damit aufgrund des biotischen Filters scheiterten.

Das letzte Kapitel (Kapitel 7) bietet Schlussfolgerungen und Perspektiven hinsichtlich des Nutzens der Ergebnisse der vorangegangenen Kapitel für den Naturschutz und für die Restitution von Grünland. Vielfach wurde angemahnt, dass Fortschritte bei der Restitution und beim Schutz von Pflanzengesellschaften nicht ohne ein Verständnis der Prozesse möglich sind, welche die Artenzusammensetzung einer Fläche bestimmen.
In den Kapiteln dieser Arbeit wurden Mechanismen erarbeitet, anhand derer sich die Artenzusammensetzungen von Grünland erklären ließen. Daher bot es sich an, die Ergebnisse unter dem Gesichtspunkt der Verwertbarkeit für den Schutz und die Restitution von Grünlandflächen zu betrachten. Besonders sollte der gegenseitige Nutzen von Naturschutzpraxis und theoretischer Forschung zu den Regeln der Artenzusammensetzung herausgearbeitet werden. Während Naturschutz-und Restitutionsprojekte den Rahmen bieten, um ökologische Theorien zu entwickeln und zu testen, kann der praktische Naturschutz von einem besseren Verständnis der Prozesse, welche die Artenzusammensetzung von Pflanzengesellschaften steuern, profitieren.
In Zukunft sollte verstärkt an der Übersetzung der Ergebnisse verschiedener biologischer Disziplinen in Maßnahmen, welche bessere Ergebnisse bei der Restitution und dem Schutz von Flächen ermöglichen, gearbeitet werden. Weitere Forschung sollte sich auf die Übertragbarkeit der Ergebnisse auf andere Flächen und Ökosysteme und auf die Validierung der in dieser Arbeit gefundenen Mechanismen beziehen.

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Appendices

Appendix 1: List of figures.

Appendix 2: List of tables.

Appendix 3: Sowing mix (species of one mix were sown together in the 10 x 10 cm subplots), provenance of seeds and selected plant functional traits of the sown species. Traits were extracted from the LEDA-traitbase (Kleyer et al. 2008) and from Ellenberg (2001). - = no database entry, x = indifferent.

	sowing mix	provenance of seeds	plant persistence	seed mass [mg]	seedbank LI	canopy height [m]	Ellenberg L	Ellenberg N
Arabis hirsuta	A	Austria	monocarpic, biannual or polyannual	0.09	0.45	0.32	7	x
Centaurea scabiosa	A	South German Scarplands	perennial	6.16	0.06	0.83	7	4
Crepis capillaris	A	South German Scarplands	monocarpic annual - perennial	0.22	0.04	0.20	7	4
Dianthus carthusianorum	A	South German Scarplands	perennial	1.03	0.00	0.26	8	2
Origanum vulgare	A	South German Scarplands	perennial	0.09	0.25	0.46	7	3
Anthyllis vulneraria	B	South German Scarplands	monocarpic annual - perennial	3.21	0.07	0.20	8	2
Buphthalmum salicifolium	B	South German Scarplands	perennial	0.46	0.42	0.33	8	3
Gentiana cruciata	B	German Alpine region	perennial	0.20	0.50	0.33	7	3
Phyteuma orbiculare	B	Austria	perennial	0.20	0.00	0.29	8	3
Teucrium botrys	B	Austria	summer annual	1.12	1.00	0.18	9	2
Ajuga genevensis	C	South German Scarplands	perennial	1.75	0.39	0.19	8	2
Galium glaucum	C	Austria	perennial	1.58	-	0.43	8	2
Inula salicina	C	South German Scarplands	perennial	0.24	0.00	0.50	8	3
Rhinanthus minor	C	Southwest Germany	summer annual	2.70	0.14	0.38	7	3
Saxifraga granulata	C	South German Scarplands	perennial	0.03	0.47	0.17	x	3

Appendix 4: Viability of seeds.

Seeds of all species were tested for viability under controlled conditions in climate chambers. We tested different germination treatments to achieve optimal germination rates. 8 Petri dishes with 25 seeds each were prepared for every species and treatment. For each species half of the samples were stratified to break dormancy prior to germination (4 weeks at 4 degrees). Temperature/light regime was chosen 22:14 °C day:night (14:10 hours). After 6 weeks ungerminated seeds of the treatment with highest germination for each species were tested for viability using tetrazolium test.

The table shows means and standard errors of germination rates at the treatment with highest germination and of the viability of seeds.

	treatment with highest germination	germination after six weeks [%]	viability
		mean ± SE	mean ± SE
Ajuga genevensis	no stratification	31.0 ± 4.7	98.0 ± 0.8
Anthyllis vulneraria	stratified	74.5 ± 2.5	91.5 ± 2.4
Arabis hirsuta	no stratification	76.0 ± 4.3	93.5 ± 2.1
Buphthalmum salicifolium	stratified	92.5 ± 1.9	97.0 ± 1.6
Centaurea scabiosa	stratified	55.5 ± 5.4	88.5 ± 5.3
Crepis capillaris	no stratification	96.0 ± 1.3	96.0 ± 1.3
Dianthus carthusianorum	no stratification	90.5 ± 1.7	91.0 ± 3.8
Galium glaucum	no stratification	40.0 ± 5.3	49.0 ± 4.9
Gentiana cruciata	stratified	96.0 ± 1.1	99.5 ± 0.5
Inula salicina	stratified	73.5 ± 2.1	76.0 ± 2.4
Origanum vulgare	stratified	85.0 ± 2.8	92.5 ± 3.1
Phyteuma orbiculare	-	0.0 ± 0.0	95.0 ± 2.0
Rhinanthus minor	stratified	5.5 ± 1.7	27.5 ± 4.6
Saxifraga granulata	no stratification	45.5 ± 5.7	93.5 ± 4.4
Teucrium botrys	no stratification	57.5 ± 3.1	74.5 ± 1.9

Appendix 5: Mean number of seedlings per quadrat (100 seeds per species sown in 2007) at different management treatments and years and survival rates to 2010. Mean numbers of flowering individuals are given in brackets when flowering occurred. Exception: number of flowering *Rhinanthus minor* individuals is not given as in each year as basically all counted individuals flowered.

	Mean number of seedlings per quadrat 2008							
	abandonment		grazing		burning		mulching once per year	
	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed
Ajuga genevensis	0.1	1.1	1.3	1.0	0.8	2.1	0.2	1.1
Anthyllis vulneraria	5.3	10.3	13.9	16.6	7.4	9.8	4.1	15.4
Arabis hirsuta	1.6	10.4	3.2	4.6	8.5	10.5	1.2	8.6
Buphthalmum salicifolium	0.8	6.5	3.7	6.9	5.0	7.8	0.2	7.8
Centaurea scabiosa	1.0	1.2	14.2	18.9	1.3	1.1	2.1	7.9
Crepis capillaris	1.5	9.8	3.8	5.8	6.6	8.9	2.0	9.1
Dianthus carthusianorum	1.7	10.2	5.1	8.2	5.1	5.5	1.1	4.4
Galium glaucum	1.7	5.6	2.0	2.6	1.0	1.4	2.9	5.4
Gentiana cruciata	0.2	2.3	1.3	1.8	1.1	1.8	0.1	2.0
Inula salicina	0.0	1.5	0.6	0.4	1.1	1.9	0.2	2.6
Origanum vulgare	1.6	9.9	3.6	4.8	5.6	9.1	1.1	9.8
Phyteuma orbiculare	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhinanthus minor	0.1	0.9	2.5	3.4	0.1	0.2	0.4	0.6
Saxifraga granulata	0.1	0.5	0.2	0.6	0.0	0.0	0.0	0.6
Teucrium botrys	0.0	0.0	0.0	0.1	0.2	0.1	0.0	0.1

	Mean number of seedlings per quadrat 2009 (mean number flowering)							
	abandonment		grazing		burning		mulching once per year	
	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed
Ajuga genevensis	0.1	0.6	0.6	0.4	1.2	0.3	0.1	0.1
Anthyllis vulneraria	0.6	1.2	6.6	7.9 (0.7)	0.9 (0.1)	1.3 (0.1)	0.9	4.2
Arabis hirsuta	1.7	6.7 (0.1)	0.5 (0.1)	0.4	2.5	2.7	0.3	3.1
Buphthalmum salicifolium	0.3	2.4	1.4	2.5	2.2	2.1	0.2	3.3
Centaurea scabiosa	0.2	0.2	4.2	4.5	0.8	1.3	0.4	1.5
Crepis capillaris	0.2	0.8	4.1	2.8	1.7	0.8	1.1	2.8
Dianthus carthusianorum	0.2	4.3	2	2.3	1.4	1.5	0.4	1.9
Galium glaucum	0.3	1.8	0.9	0.5	0.3	0.4	0.9	1.6
Gentiana cruciata	0	0.1	0	0	0	0	0.1	0.1
Inula salicina	0	0.4	0.2	0.1	0.8	0.7	0	0.2
Origanum vulgare	0.8	4.6	0.5	0.3	0.2	0.4	0.4	3.5
Phyteuma orbiculare	0	0	0	0	0	0	0	0
Rhinanthus minor	0.3	0.9	10.9	10.8	0	0.2	0.6	2.5
Saxifraga granulata	0.1	0	0	0	0	0	0	0
Teucrium botrys	0	0	0.1	0.1	0.1	0.1	0.1	0

Appendix 5: continued

	Mean number of seedlings per quadrat 2010 (mean nb. flowering)							
	abandonment		grazing		burning		mulching once per year	
	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed
Ajuga genevensis	0	0.1	0.1	0.1	0.1	0	0	0
Anthyllis vulneraria	0	0.1	1.6 (0.8)	2.8 (2.1)	0.2	0.3	0.6 (0.1)	0.3 (0.1)
Arabis hirsuta	0.2	2.6	0.6	0.2	0.2	0.3	0.1	0.4
Buphthalmum salicifolium	0.1	0	0.2	0.3	0.3	0.1	0	0.3
Centaurea scabiosa	0.1	0.1	0.5	0.5	0	0	0	0.3
Crepis capillaris	0.1	0.2	0.1	0.4	0.1	0	0.1	0.4
Dianthus carthusianorum	0.1	0.6	0.4	0.2	0.3	0.1	0	0.3
Galium glaucum	0.1	0.4	0.1	0	0	0	0	0
Gentiana cruciata	0	0	0	0	0	0	0	0
Inula salicina	0	0	0	0	0	0	0	0
Origanum vulgare	0	0.3	0.1	0	0.1	0	0.1	0.8
Phyteuma orbiculare	0	0	0	0	0	0	0	0
Rhinanthus minor	0	0.7	13.8	13.5	0	0	0.2	4.2
Saxifraga granulata	0	0	0	0	0	0	0	0
Teucrium botrys	0	0	0	0	0	0	0	0

	Mean survival rates of seedlings per quadrat to 2010							
	abandonment		grazing		burning		mulching once per year	
	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed	undisturbed	disturbed
Ajuga genevensis	0	7.7	8.3	2.3	3.3	0	0	0
Anthyllis vulneraria	0	0.2	9.6	11.5	1.8	3.3	19.7	1.9
Arabis hirsuta	4.4	21	12.3	5.6	3.2	2.3	4.8	4.2
Buphthalmum salicifolium	12.5	0	10.3	6	3.8	2.3	0	3.3
Centaurea scabiosa	2.4	6.3	2.7	3.2	0	0	0	2.2
Crepis capillaris	3.7	2.6	0.6	6.9	0.6	0	7.2	4.1
Dianthus carthusianorum	5	4	7.9	1.8	2.6	3.8	0	5
Galium glaucum	3.6	5.8	7.1	0	0	0	0	0
Gentiana cruciata	0	0	0	0	0	0	0	0
Inula salicina	0	0	0	0	0	0	0	0
Origanum vulgare	0	3.3	3.3	0	2	0	3.3	14.1
Phyteuma orbiculare	0	0	0	0	0	0	0	0
Rhinanthus minor *	0	9.4	316.9	87	0	0	22.2	92.8
Saxifraga granulata	0	0	0	0	0	0	0	0
Teucrium botrys	0	0	0	0	0	0	0	0

* for *Rhinanthus minor* is an annual species which reproduces by seeds every year. Thus, the "survival rate" of 316.9 indicates in this case that the population at the grazing treatment increased by 3.2 times relative to the highest seedling numbers reached in the previous years and so on.

Appendix 6: Means ± SE of initial seedling numbers and neighbourhood characteristics for plots without vital individuals (dead) and plots with vital individuals (alive) for *Rhinanthus minor* and *Anthyllis vulneraria*. Mann-Whitney U-tests were performed to test for significant differences between means. p<0.05=*, p<0.01=**, p<0.001=***.

		Rhinanthus minor				***Anthyllis vulneraria***			
		dead n= 27	alive n= 15	U	p	dead n= 56	alive n= 17	U	p
	number of seedlings 2008	1.3 ± 0.13	1.5 ± 0.31	188.0	0.649 n.s.	3.43 ± 0.31	5.35 ± 0.68	277.5	0.009 **
spring measurements	height of vegetation	6.0 ± 0.38	4.7 ± 0.45	133.5	0.066 n.s.	5.25 ± 0.25	4.88 ± 0.37	426.0	0.506 n.s.
	cover vegetation	74.6 ± 2.92	70.7 ± 4.78	184.0	0.625 n.s.	71.59 ± 1.88	75.88 ± 2.82	393.5	0.278 n.s.
	cover moss layer	6.6 ± 1.44	8.9 ± 3.14	196.5	0.874 n.s.	5.68 ± 0.94	5.35 ± 1.87	405.5	0.353 n.s.
	height moss layer	0.05 ± 0.04	0.07 ± 0.07	196.5	0.796 n.s.	0.06 ± 0.03	0.01 ± 0.00	360.5	0.023 *
	cover litter layer	16.7 ± 2.57	16.0 ± 3.64	185.0	0.625 n.s.	15.75 ± 1.29	15.24 ± 2.52	462.0	0.852 n.s.
	height litter layer	0.41 ± 0.11	0.01 ± 0.00	135.0	0.021 *	0.26 ± 0.07	0.13 ± 0.08	435.5	0.427 n.s.
	bare ground	29.7 ± 3.57	30.1 ± 4.45	201.5	0.979 n.s.	36.02 ± 2.01	27.29 ± 2.90	324.5	0.046 *
summer measurements	sum of species cover values	105.0 ± 4.95	111.2 ± 4.88	155.0	0.212 n.s.	102.68 ± 2.69	108.37 ± 4.93	402.5	0.337 n.s.
	height of vegetation	10.7 ± 1.36	9.8 ± 1.64	185.5	0.654 n.s.	9.43 ± 0.79	8.41 ± 1.04	448.5	0.718 n.s.
	mean weighted Ellenberg L	7.1 ± 0.04	7.2 ± 0.06	161.0	0.276 n.s.	7.08 ± 0.04	6.98 ± 0.10	408.0	0.375 n.s.
	mean weighted Ellenberg N	3.9 ± 0.11	3.6 ± 0.09	130.0	0.057 n.s.	3.8 ± 0.08	3.7 ± 0.16	431.0	0.557 n.s.
	proportion of legume cover	0.10 ± 0.01	0.13 ± 0.02	166.0	0.338 n.s.	0.11 ± 0.01	0.08 ± 0.01	318.0	0.039 *
	species richness	19.0 ± 0.52	23.3 ± 1.02	71.5	0.001 **	19.71 ± 0.40	19.76 ± 1.04	453.0	0.763 n.s.
	Eveness	2.6 ± 0.04	2.6 ± 0.06	178.0	0.520 n.s.	2.53 ± 0.02	2.54 ± 0.05	461.5	0.850 n.s.
Grime´s strategy types	C	0.31 ± 0.01	0.28 ± 0.01	130.0	0.057 n.s.	0.31 ± 0.01	0.29 ± 0.01	360.0	0.130 n.s.
	S	0.43 ± 0.01	0.48 ± 0.02	130.0	0.057 n.s.	0.43 ± 0.01	0.47 ± 0.02	346.0	0.090 n.s.
	R	0.26 ± 0.01	0.24 ± 0.01	140.0	0.101 n.s.	0.26 ± 0.01	0.24 ± 0.01	389.0	0.256 n.s.
community weighted means	canopy height	0.34 ± 0.01	0.33 ± 0.01	182.0	0.590 n.s.	0.33 ± 0.01	0.33 ± 0.01	434.0	0.584 n.s.
	SLA	21.4 ± 0.25	21.2 ± 0.35	173.0	0.439 n.s.	21.30 ± 0.20	21.30 ± 0.41	475.0	0.990 n.s.

Appendix 7: Means ± SE of plots with and without survivors over eight species for neighbourhood characteristics. Mann-Whitney U-tests were performed to test for significant differences between means of 8 species for plots with survivors versus plots without vital individuals.

		mean (± SE) of 8 species		Mann-Whitney U test	
		plots with no survivors	plots with survivors	U	p
	number of seedlings 2008	2.2 ± 0.38	3.1 ± 0.62	20	0.208 n.s.
	height of vegetation	**5.5 ± 0.11**	**4.4 ± 0.47**	**9**	**0.015 ***
	cover of vegetation	71.3 ± 1.70	59.0 ± 7.28	23	0.345 n.s.
	cover of moss layer	5.9 ± 0.28	4.9 ± 1.22	27	0.600 n.s.
spring measurements	height of moss layer	0.1 ± 0.00	0.1 ± 0.03	22	0.293 n.s.
	cover of litter layer	16.3 ± 0.72	15.1 ± 2.40	28	0.674 n.s.
	height of litter layer	**0.3 ± 0.03**	**0.1 ± 0.06**	**10**	**0.020 ***
	bare ground	32.5 ± 0.83	38.4 ± 7.62	29	0.753 n.s.
summer measurements	sum of species cover values	103.6 ± 0.52	109.2 ± 3.49	19	0.172 n.s.
	height of vegetation	10.1 ± 0.25	10.5 ± 0.96	30	0.834 n.s.
	Ellenberg L	7.1 ± 0.02	7.1 ± 0.05	26	0.529 n.s.
	Ellenberg N	3.7 ± 0.04	3.6 ± 0.09	22	0.294 n.s.
	proportion of legume cover	0.1 ± 0.00	0.1 ± 0.01	24	0.400 n.s.
	species richness	**19.6 ± 0.21**	**21.0 ± 0.52**	**7**	**0.009 ****
	eveness	2.5 ± 0.01	2.5 ± 0.02	29	0.753 n.s.
	C	0.3 ± 0.00	0.3 ± 0.01	28	0.674 n.s.
Grime´s strategy types	S	0.4 ± 0.00	0.5 ± 0.01	25	0.462 n.s.
	R	0.2 ± 0.00	0.2 ± 0.01	19	0.172 n.s.
community weighted means	canopy height	0.3 ± 0.00	0.3 ± 0.01	32	1.000 n.s.
	SLA	21.2 ± 0.10	20.9 ± 0.33	30	0.834 n.s.

Appendix 8: Attribute distributions and mean trait values of indicator species of ancient and recent grasslands tested for significant differences against mean trait values and attribute distributions in the residual species pool (Mann-Whitney U-tests/Chi²-tests, N= 110).

		Test for significant divergences from residual species pool									
		ancient grassland indicators					recent grassland indicators				
	scale	n ancient grassland indicators	n residual species pool	U	Chi	p	n recent grassland indicators	n residual species pool	U	Chi	p
seed number	metric	12	68	243.0		0.026 *	32	48	717.0		0.616 n.s.
terminal velocity	metric	17	81	498.0		0.074 n.s.	35	63	698.5		0.003 **
number of dispersal vectors	metric	16	86	634.5		0.605 n.s.	38	64	1065.0		0.273 n.s.
anemochorous dispersal	yes /no	16	86		3.1	0.078 n.s.	38	64		1.4	0.239 n.s.
zoochorous dispersal	yes /no	16	86		1.6	0.204 n.s.	38	64		2.3	0.131 n.s.
epizoochorous dispersal	yes /no	16	86		0.6	0.435 n.s.	38	64		1.6	0.206 n.s.
endozoochorous dispersal	yes /no	16	86		0.0	0.960 n.s.	38	64		0.0	0.881 n.s.
hemerochorous dispersal	yes /no	16	86		1.6	0.207 n.s.	38	64		4.6	0.031 *
seed mass	metric	16	89	711.5		0.996 n.s.	39	66	1233.0		0.720 n.s.
germination season	spring, all year, autumn	17	87		1.3	0.531 n.s.	39	65		1.9	0.378 n.s.
minimum germination temperature	metric	7	51	299		0.031 *	27	31	299		0.054 n.s.
maximum germination temperature	metric	7	56	148.0		0.291 n.s.	29	34	388.0		0.145 n.s.
seed dormancy	no, no/physiological, physiological, physical	13	77		0.8	0.854 n.s.	37	53		2.9	0.400 n.s.
canopy height	metric	17	93	346.5		0.000 ***	40	70	957.5		0.008 **
leaf distribution	rosette, semi-rosette, regularly	17	93		5.8	0.056 n.s.	40	70		6.4	0.041 *
specific leaf area (SLA)	metric	16	92	668.0		0.556 n.s.	40	68	1137.5		0.157 n.s.
leaf dry matter content (LDMC)	metric	16	82	625.0		0.766 n.s.	39	59	1056.5		0.495 n.s.
minimum connection to mother plant	1-2 years, >2 years	16	82		1.3	0.262 n.s.	37	61		0.2	0.682 n.s.
lifespan	long (perennials), short (annuals + biennials)	17	93		0.2	0.692 n.s.	40	70		0.0	1.000 n.s.
seedbank longevity index	metric	16	91	599.5		0.260 n.s.	40	67	1178.0		0.295 n.s.
leaf phenology	vernal, aestival, partly evergreen, evergreen	17	93		1.1	0.776 n.s.	40	70		2.2	0.527 n.s.
woodiness	non-woody, semi-woody, woody	17	93		0.2	0.900 n.s.	40	70		0.1	0.968 n.s.
number of budbank-layers	metric	17	91	634.5		0.312 n.s.	40	65	1098.5		0.052 n.s.
maximum lateral spread per year	<100mm, 100-250mm, >250mm	17	92		4.2	0.120 n.s.	40	69		7.3	0.025 *
earliest month of seed shedding	metric	17	90	583.0		0.102 n.s.	38	69	1265.0		0.752 n.s.
latest month of seed shedding	metric	17	90	552.0		0.062 n.s.	38	69	1188.5		0.412 n.s.
seed shedding duration	metric	17	90	559.0		0.073 n.s.	38	69	1268.5		0.777 n.s.
Ellenberg indicator value for light	ordinal	17	90	511.0		0.019 *	40	67	1267.0		0.610 n.s.
Ellenberg indicator value for moisture	ordinal	16	80	493.5		0.828 n.s.	33	54	833.0		0.585 n.s.
Ellenberg indicator value for reaction	ordinal	14	67	405.5		0.399 n.s.	30	51	694.0		0.461 n.s.
Ellenberg indicator value for nitrogen	ordinal	16	80	340.0		0.002 **	32	64	607.0		0.001 **
grass (or herb)	yes /no	17	93		0.0	0.950 n.s.	40	70		0.8	0.375 n.s.
non-legume (or legume)	yes /no	17	93		1.6	0.204 n.s.	40	70		8.5	0.003 **
growth form	therophyte, hemicryptophyte, geophyte, chamaephyte, liana	17	93		2.6	0.626 n.s.	40	70		5.8	0.215 n.s.
% C Crime	0-100%	9	56	106.5		0.004 **	28	37	257.0		0.000 ***
% S Grime	0-100%	9	56	107.5		0.005 **	28	37	209.5		0.000 ***
% R Grime	0-100%	9	56	182.5		0.180 n.s.	28	37	339.0		0.016 *

Appendix 9: Comparison of biotic environment (community weighted mean values for metric traits/percentage cover of species with certain trait attributes) between ancient and recent grasslands for traits that separated indicator species from the species pool. Means and standard errors, Mann-Whitney U and p-values are given (ancient grassland plots n= 50, recent grassland plots n= 40).

	mean ± SE grasslands ancient	mean ± SE grasslands recent	Mann-Whitney U	p-value	
Ellenberg indicator value for light	7.6 ± 0.0	7.5 ± 0.0	638.0	0.003	**
Ellenberg indicator value for nitrogen	2.8 ± 0.0	3.1 ± 0.0	347.5	0.000	***
canopy height	0.3 ± 0.0	0.4 ± 0.0	318.0	0.000	***
terminal velocity	2.1 ± 0.0	2.4 ± 0.0	172.0	0.000	***
seed number	1569.2 ± 67.5	2551.0 ± 183.2	316.0	0.000	***
minimum germination temperature	9.5 ± 0.1	8.6 ± 0.2	491.0	0.000	***
% lateral spread < 100mm/year	32.4 ± 1.0	35.7 ± 1.6	798.0	0.101	n.s.
% lateral spread 100-250 mm/year	51.9 ± 1.2	45.4 ± 1.7	597.5	0.001	**
% lateral spread > 250 mm/year	15.7 ± 0.9	18.8 ± 1.9	934.5	0.595	n.s.
% hemerochorous dispersal	43.5 ± 1.2	52.7 ± 1.7	529.5	0.000	***
% C strategy affiliation	19.8 ± 0.8	27.2 ± 0.7	308.0	0.000	***
% S strategy affiliation	65.5 ± 1.1	54.2 ± 1.0	255.0	0.000	***
% R strategy affiliation	14.6 ± 0.4	18.6 ± 0.7	443.0	0.000	***
% legumes	24.8 ± 1.2	32.8 ± 2.0	627.0	0.002	**
% leaves distributed regularly	15.7 ± 0.9	20.7 ± 1.1	550.5	0.000	***
% rosettes	13.8 ± 0.9	9.3 ± 0.9	566.0	0.000	***
% semi-rosettes	70.5 ± 0.9	70.0 ± 1.2	990.0	0.935	n.s.

Dank

Allen voran möchte ich mich herzlich bei meinem Doktorvater Prof. Dr. Peter Poschlod für das interessante Thema, die Betreuung der Arbeit und für die Möglichkeit der Teilnahme an interessanten Tagungen und Workshops bedanken.

Bei Prof. Dr. Christine Römermann bedanke ich mich für die Bereitschaft das Zweitgutachten zu übernehmen und selbstverständlich auch für Rat und Hilfe bei (Statistik)fragen, ebenso wie für wertvolle Diskussionen und Kommentare zur Arbeit.

Ein großer Teil dieser Arbeit wurde im Rahmen des „ASSEMBLE“-Projektes durchgeführt und durch die European Science Foundation und die DFG-EuroDIVERSITY 040 (PO 491/5-1) unterstützt. Ich möchte allen Mitarbeitern dieses Projektes für die gute Zusammenarbeit und die vielen hilfreichen Diskussionen danken. Besonders möchte ich Dr. Markus Bernhardt-Römermann für die Unterstützung bei der RLQ-Auswertung und seine stete Hilfsbereitschaft danken.

Ein großer Dank geht an Prof. Karl-Friedrich Schreiber, der 1975 die „Offenhaltungsversuche Baden-Württemberg“ ins Leben rief und an die LEL Schwäbisch Gmünd, welche die Arbeit ebenfalls unterstützte, und mir die Freilandarbeit auf den Projektflächen der „Offenhaltungsversuche Baden-Württemberg“ ermöglichten.

Bei Philipp Kollmar und Josef Simmel möchte ich mich für ihre tatkräftige Mitarbeit im Freiland bedanken. Ebenso ist den studentischen Hilfskräften gedankt, welche mich im Laufe der letzten Jahre unterstützten: Michaela Adlmüller, Maria Hanauer, Martin Leipold, Fabian Kellermeier und Simone Tausch.

Meinen jetzigen und ehemaligen Kollegen der AG Poschlod danke ich für die schöne gemeinsame Zeit und für die angenehme Arbeitsatmosphäre! Insbesondere möchte ich mich bei Christina Meindl, PD. Dr. Christoph Reisch und Dr. Maik Bartelheimer für die thematische, praktische und freundschaftliche Begleitung während der Promotion bedanken.

Ein herzlicher Dank geht an meine Eltern, welche mein Studium und die Promotion stets unterstützt haben.